ABSTRACT

The eastern hognose snake (*Heterodon platirhinos*) is an understudied species of
increasing conservation concern, especially in the northeastern portion of its range.
Conservation and management efforts often rely on ecological information to guide best
practices when dealing with vulnerable and/or cryptic species. A radiotelemetry study
was initiated at Cape Cod National Seashore, Barnstable County, Massachusetts on *H.
platirhinos* in an effort to increase the understanding of spatial ecology, habitat selection,
and associated natural history attributes. Sixteen adult *H. platirhinos* were tracked over
two years yielding a total of 413 relocations. We observed a large variation in home
range size among individuals (MCP mean = 31 ha, MCP range = 1-209 ha) and seasonal
differences in movements between sexes with female movements peaking in July, and
male movements peaking in September. Estimates of daily movements averaged 25.9
m/d and were less than estimates derived from other studies of *H. platirhinos*. Also
contrary to other studies, females showed a high rate of reproduction with oviposition
taking place in late-June to early-July. Probability of occurrence increased with certain
physical and vegetative characteristics (grass, leaf litter) and decreased with others (open
soil, cranberry). We documented the first instance of hibernaculum site fidelity in this
species.

MONTCLAIR STATE UNIVERSITY

Ecology of the Eastern Hognose Snake (*Heterodon platirhinos*) at

Cape Cod National Seashore, Barnstable County, Massachusetts

by

Scott W. Buchanan

A Master's Thesis Submitted to the Faculty of

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In Partial Fulfillment of the Requirements

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ECOLOGY OF THE EASTERN HOGNOSE SNAKE (*HETERODON PLATIRHINOS*)

AT CAPE COD NATIONAL SEASHORE, BARNSTABLE COUNTY,

MASSACHUSETTS

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CHAPTER I

REPRODUCTIVE ECOLOGY, THERMAL ECOLOGY, AND ACTIVITY OF THE

EASTERN HOGNOSE SNAKE (*HETERODON PLATIRHINOS*) AT CAPE COD

NATIONAL SEASHORE, BARNSTABLE COUNTY, MASSACHUSETTS

Introduction

Radiotelemetry has greatly improved our understanding of snake spatial ecology and

habitat use over the past several decades (Fitch and Shirer 1971, Prior and Weatherhead

1996, Reinert 1984a, Sperry and Weatherhead 2009). Although the primary hypotheses

being tested vary from study to study, supplemental natural history information is often

compiled opportunistically during radiotelemetry, resulting in novel information and

additional hypotheses. Observations and measurements relating to activity/dormancy,

interspecific interactions (i.e., predation, diet), reproductive ecology, and physiological

ecology are often made where possible (Cunnington and Cebek 2005, Green and Cobb

2011, Plummer and Mills 2010). These all represent valuable data when attempting to

understand a species' evolutionary strategies for survival and reproduction and, in turn,

for guiding conservation and management efforts.

Heterodon platirhinos Latreille (Eastern Hognose Snake) is a species of increasing

conservation concern, especially in the northeastern United States (Klemens 1993,

NEPARC 2010, Seburn 2009, Therres 1999). Of the five states in the Northeast where

H. platirhinos occurs, it currently has "listed" conservation status in four (Connecticut,

New Hampshire, New York, and Rhode Island). In Massachusetts, officials are currently

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soliciting information on the species to better assess its status in the state (L. Erb, Massachusetts Division of Fisheries and Wildlife, Westborough, MA, 2011 pers. comm.). Noted declines are believed to be the result of direct anthropogenic pressures including habitat loss and fragmentation, road mortality, environmental degradation, and intentional killing (Ernst and Ernst 2003, Gibbons et al. 2000).

Although there are many accounts in the literature that contain some facet of *H. platirhinos* natural history, these consist largely of scattered encounters from throughout its range and tend to be anecdotal in nature. Relatively few studies have compiled quantitative ecology and natural history information for single populations of the snake over multiple years. Probably contributing to this dearth of information is the species' cryptic nature and the fact that throughout most of its range *H. platirhinos* appears to occur in low population densities relative to sympatric snake species (Fitch 1993, Ford 1991). Among the variety of habitat types in which *H. platirhinos* is found, it occurs in greatest densities in well drained, sandy soils (Conant 1938, Fitch 1993). Barrier beach and dune ecosystems appear to contain the highest population densities due to abundant prey (primarily toads) and expanded niche opportunity as a result of reduced snake fauna (Brady 1925, Scott 1985, Stewart and Rossi 1981). The northern tip of the Cape Cod peninsula consists of an expansive, early successional sand dune landscape that serves as ideal habitat for *H. platirhinos*. A two-year radiotelemetry study, initially designed to gather data on spatial ecology and habitat use, resulted in a number of significant observations and measurements related primarily to reproductive ecology and activity.

Materials and Methods

Study area

  Cape Cod National Seashore (CCNS) is located in Barnstable County in southeastern Massachusetts. Cape Cod is a long, narrow peninsula that extends out into the Atlantic Ocean. The study was conducted at the outermost portion (northern terminus) of the peninsula in an approximately 1,800 hectare section of the park known as the Province Lands. Whereas the rest of Cape Cod consists of glacial moraine and outwash deposits of sand, silt, and clay left behind by Pleistocene glaciers, the Province Lands consist entirely of postglacial deposits of eroded coastal sediments carried north by long-shore currents. Over time, predominant marine and aeolian forces have given the hook-like tip of the peninsula its distinctive spiral shape and formed the parabolic dune landscape that exists there today (Uchupi et al. 1996). Soils in the Province Lands consist almost entirely of sand. Elevations range from approximately 0 to 33 meters above sea level. Intensive land use by European settlers, which included clearing of forest for fuel and grazing, and the prevalent xeric conditions have resulted in a patchy mosaic of early successional communities including open dune soil crusts, heathland-like assemblages, dune grasslands, shrubs, and scrub woodlands. Upland forest types are dominated by *Pinus rigida,* with some *Quercus velutina,* and *Q. ilicifolia.*   Dune grasslands are dominated by *Ammophila breviligulata* and *Deschampsia flexuousa*. Heathland-like communities consist of mats of colonizing lichens, dwarf shrubs, and *Toxicodendron radicans*. The grasslands and heathlands are often interspersed with single shrubs or mixed shrub patches of *Prunus maritima*, *Prunus serotina*, *Morella pensylvanica, and Rosa rugosa*. Dune slack wetlands occur where wind-scour has lowered the surface elevation to where

it seasonally intersects the groundwater table. These wetlands are relatively diverse

systems, but the most abundant species include *Vaccinium macrocarpum*, *Morella*

pensylvanica, *Kalmia angustifolia*, *V. corymbosum*, and *Juncus greenei* (Smith et al.

2008). Tidally influenced salt marshes occupy portions of the land-sea interface.

Radiotelemetry

   Individual *H. platirhinos* were located by active searches, incidental encounters by park

staff, and in proximity to other radiotracked snakes. Relatively few snakes were found

near radiotracked snakes (see Results), placating concerns over population sampling bias

due to a narrow set of habitat preferences among individuals. Snakes weighing more

than 100g and showing no signs of disease or injury were considered for radiotracking.

Radio transmitters included models SI-2T 11g, SI-2T 9g, and SB-T 5g produced by

Holohil Systems Ltd (Carp, Ontario, Canada). Radios were surgically implanted using

techniques modified from Reinert and Cundall (1982), as detailed in Calle et al. (2005).

Transmitters did not exceed 4.5% of snake body mass (mean = 3.2% , SE = 0.29, *n* = 16

individuals). All snakes were held in post-operative veterinary quarantine for a minimum

of 24 hours until they exhibited signs of full recovery. There was no mortality associated

with surgery. Following release at their original points of capture, snakes were

radiotracked using a Telonics TR-4 radio receiver (Telonics Inc., Mesa, AZ) and a three-

point Yagi antenna. Multiple studies have indicated that *H. platirhinos* are

predominantly diurnal (Platt 1969, Plummer and Mills 2000). Thus, all relocations

occurred during daylight hours only.

Data Collection

  At each snake relocation, data were collected on body temperature, geographic

location, microclimate (at snake-level and ambient), and snake behavior (hereafter

referred to as activity). In addition, body mass was measured to the nearest 1 g

approximately once every two weeks using a Pesola^{TM} spring scale. Monitoring body

mass on a regular basis allowed for an approximation of oviposition dates. If it was

suspected that a female was gravid, frequency of body mass measurement was increased

to more accurately estimate oviposition dates. Body temperature (T_b) was estimated to

the nearest 0.5 °C by measuring the pulse interval of the temperature-sensitive

transmitters. A pulse interval was obtained by timing the length (in seconds) between ten

pulses and calculating an average. This value was applied to a pre-calibrated curve

provided by the transmitter manufacturer to obtain T_b. Geographic location was recorded

in Universal Transverse Mercator (UTM) coordinates (North American Datum of 1983)

using a Garmin GPS 72 handheld global positioning system receiver (Garmin

International Inc., Olathe, KS). Microclimate variables were measured using a Kestrel

2500 Pocket Wind Meter (Nielsen-Kellerman, Boothwyn, PA). Temperature (to the

nearest 0.1 °C), relative humidity (to the nearest 0.1%), and average wind speed (to the

nearest 0.1 m/s) were measured at ambient level (~ 1.0 m directly above the encounter

location of the snake) and at snake-level (within 20 cm of the encounter location, and

approximately 3cm above the ground) during the time of each snake relocation. Snake

activity was considered as either "active" or "inactive." Active behaviors were those

where snakes were exposed above vegetation; this included observations of actively

moving, burrowing, feeding, copulating, and coiled on the surface. Inactive behaviors

were those where snakes were underground or concealed under vegetation (see Plummer and Mills 2010). Fifty-nine relocations (~14.3% of total) were not characterized into either category due to insufficient data. These relocations were characterized as "unknown" and excluded from activity analysis.

Statistical Analysis

Reptiles often exhibit strong differences in activity and use of habitat between intraspecific reproductive classes (Millar and Blouin-Demers 2011, Reinert 1984b, Wund et al. 2007). In radiotelemetry studies, females are often subdivided into gravid and non-gravid classes. Due to a limited number of radiotracked non-gravid females ($n = 2$) however, no subdivision was carried out. Unless otherwise noted, all females were considered as one class.

Descriptive statistics were calculated for year-round T_b data, and for T_b data restricted to the activity season (i.e., excluding measurements taken when snakes were in hibernacula). Linear regression and quadratic regression were used to assess relationships between T_b and microclimate variables (snake-level temperature and ambient air temperature) for all relocations. The difference in T_b and ambient air temperature (T_{air}) was calculated for all relocations and used to assess relationships with microclimate variables and activity. Linear regression was used to assess the relationship between T_{air} (as the x variable) and the difference between T_b and T_{air} (as the y variable). T_b - T_{air} was considered a superior metric (as opposed to T_b) for assessing the relationship between variation in body temperature and activity as it accounts for differences in T_{air} among measurements and because it met the assumptions of normality and homogeneity of variances required for parametric tests (whereas T_b did not). Mean $T_b - T_{air}$ was

calculated for all active and all inactive observations for each snake and compared using a paired t test. Similar to Plummer and Mills (2010), a nonparametric Wilcoxon test was used to assess differences in mean T_b between sexes. For both analyses, only measurements taken during the activity season were used.

In order to investigate seasonal differences in diel activity, proportions of active relocations were grouped by hours after sunrise. We hypothesized that snakes would tend to be more active during the early morning and evening hours in the warmer months, and more active in the intervening hours during the cooler months; this in an effort to maintain optimal T_b in varying environmental conditions. Thus, ambient air temperature from all activity season relocations containing data (May 13 – October 2) was smoothed using a $\pm$ 5-day sliding average (both years combined). The apex of this curve was selected as the average warmest day of the year (~25 July). The "warm season" was considered as the range of dates, with 25 July as the midpoint, that included 50% of all dates considered (19 June – 30 August). The "cool season" was considered the days of the activity season which fell outside of this range (13 May – 18 June and 31 August – 2 October). Proportion of active relocations were also separated by sex and grouped by month.

Mixed effects logistic regression was employed to assess the relationship between snake activity status and selected microclimatic and temporal variables. Snake-level microclimatic variables were not considered in regression analysis due to high correlation with ambient variables and based on the rationale that the snake-level variables would be more likely to represent a transient (and therefore non-representative) condition present at the location of an actively moving snake. We assessed the fit for each remaining variable

using both a standard logistic and a quadratic function, and for each variable for each sex we retained the functional relationship that best fit the data as assessed via Akaike's Information Criterion (AIC) analyses. We considered all possible subsets of retained variables as candidate mixed effects logistic regression models. We ranked models using AIC scores corrected for small sample sizes (AIC_c), and models with the lowest AIC_c score were considered most supported (Burnham and Anderson 2002). All means are reported $\pm$ SE, and tests were considered significant at α=0.05. JMP version 8.0 and 9.0 (SAS Institute Inc., Cary NC) and R version 2.13.2, (R Development Core Team, Vienna, Austria) were used for statistical analyses.

Results

Radiotelemetry

Sixteen snakes (10 females, 6 males) were radiotracked during the two year duration of the study (Figure 1.1). Seven individuals were located by actively searching through specific cover types present at the study site, 7 were located via incidental encounters by park staff, and 2 were found in proximity to other radiotracked snakes. Individuals were relocated approximately once every 4 days from the beginning of May to the end of August (mean = 4.17 days, SE = 0.13, n = 315 relocations) and approximately once every 12.5 days during September and October (mean = 12.46 days, SE = 1.08, n = 54 relocations). Snakes were also radiotracked when possible during late fall and early spring. Duration of radiotracking averaged 191 calendar days per snake (mean = 191.4 days, SE = 47.0, range = 1-553 days, n = 16 individuals), and individuals were relocated on average ~26 times (mean = 25.8 days, SE = 4.8, n = 16 individuals) prior to

death/signal loss/end of study. A total of 413 relocations were logged over two years. Five snakes were radiotracked during both years (Table 1.1).

Permanent signal loss occurred with 4/16 individuals (25%). This may have been a result of transmitter failure, predation, snakes inhabiting topography or vegetation that diminished signal strength, or long-distance movements beyond the range of the receiver. Of note however, is the fact that one of these four individuals (snake M) was relocated in 2011 during radiotelemetry associated with a related study. Thus, only the later two hypotheses would explain this observation. Also of interest was a separate occasion in which only a transmitter was found. Similar to Lagory et al. (2009) (another radiotelemetry study of *H. platirhinos*), this occurred recently after release from surgery (approximately 6 days in our study). This could have been the result of predation or the active expulsion of the transmitter by the snake through a fresh suture incision.

Three snakes (18.8% of all individuals) were confirmed to have died during the course of the study, all in 2009. On 31 May 2009 a female measuring 500 mm SVL, 595 mm total length (TL), and weighing 156g (two weeks prior to being predated) was found predated by a *Coluber constrictor* Linnaeus (Racer).   X-ray imaging confirmed the presence of the transmitter in the digestive track of the *C* . *constrictor*. The *C. constrictor* measured 1140 mm SVL, 1480 mm TL, and weighed 768 g immediately after capture. The estimated relative prey mass (i.e., the prey mass divided by predator mass (excluding prey mass)) was 25.5% and the relative prey length was 40.2%. On 5 July 2009 a gravid female was found predated by what may have been a raptor. The partially eaten carcass was found on top of an old pine snag approximately one meter above the ground. On 11 July 2009 a female was found to have died during oviposition. The posterior half of her

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body was buried below loose sand and the anterior half of her body was raised above the sand. There was sand on the head of the snake suggesting recent burrowing. Subsequent examination of the nest site revealed that she had deposited 17 eggs at a depth of approximately 15 cm. Necropsy revealed an additional 6 eggs inside the body. Dissection revealed that the stomach was empty and the transmitter was moving freely between the coelem wall and the muscle layer. The suture was intact and there appeared to be no abscess or infection at the site of the transmitter. There was no observable internal cause of death. The fate of the 17 deposited eggs was unknown when monitoring ceased at the end of August that year.

Activity

A total of 335 (81.1% of total) relocations were characterized as active or inactive and were used in activity analyses. The percent of active relocations varied between sexes with females active during 109 of 225 relocations (48.4%), and males active during 38 of 110 relocations (34.5%). The proportion of active relocations varied by hours after sunrise and between seasons. The time period with the greatest proportion of active relocations was the third hour (2-3) after sunrise, though this should be interpreted with caution because of small sample size ($n = 5$). The time period with the smallest proportion of active relocations was the twelfth hour (11-12) after sunrise. There were no active relocations recorded during the second hour (1-2) or beyond the thirteenth hour (12-13) (though sample size for these groups is also small) (Figure 1.2a). The proportion of greatest activity occurred in the fourth hour (3-4) in the warm season, and in the fifth hour (4-5) in the cool season (Figure 1.2b). Analysis of seasonal activity was restricted to the months of May-October ($n = 329$ relocations, 79.7% of all relocations) due to

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infrequency of relocation in the early spring and late fall. The greatest proportion of

active female relocations occurred in July and August, though these proportions were

similar to those in May and June. For males, the greatest proportion of active relocations

occurred in September with activity in May-August less than that observed in females

(Figure 1.3).

 The mixed effects logistic regression model with the strongest support for female

activity included a standard logistic relationship for ambient relative humidity, a

quadratic relationship for ambient air temperature, and a quadratic relationship for hours

after sunrise (AIC$_c$ = 260.69, ω = 0.68). The model with the strongest support in

describing activity status for males was the model that included a standard logistic

functional relationship for ambient relative humidity and a quadratic relationship for

ambient air temperature (AIC$_c$ = 120.11, ω = 0.39).

Body Temperature

 Figure 1.4 is a conceptual model showing the relationships between ambient air

temperature, body temperature, and activity.   A total of 363 T$_b$ observations were taken

in two years (Table 1.2). T$_b$ ranged from 5.5 – 39.5 ℃ with the majority of

measurements (264/363, 72.3%) occurring in the 27.5-37.5 ℃ range (Figure 1.5). There

was no statistical difference in T$_b$ between sexes (Z = 0.95, P = 0.34, n = 13). Figure 1.6

shows the relationship between snake-level, ambient, and body temperatures throughout

the year. There was a significant positive correlation between T$_b$ and both ambient and

snake level temperatures (ambient r^2 = 0.613, P < 0.001, slope = 0.88; snake level r^2 =

0.653, P < 0.001, slope = 0.84) (Figure 1.7). Quadratic regression however, revealed a

stronger significant positive correlation between T$_b$ and the same two variables (ambient

$r^2 = 0.679$, $P < 0.001$; snake level $r^2 = 0.737$, $P < 0.001$). When T_b - T_{air} was plotted over the entire range of T_{air}, there is no statistical relationship between the two variables ($r^2 = 0.029$, $P = 0.002$, slope = -0.12). However, when only a subset of data is considered in which T_{air} is greater than 22ºC, a negative correlation emerges ($r^2 = 0.4247$, $P < 0.001$, slope = -0.77) (Figure 1.8). A total of 292 T_b measurements (excluding observations categorized as "unknown" and observations taken while snakes were in hibernacula) were retained for 13 individuals and used in comparative analyses to test for differences between active and inactive observations. Mean active T_b was 30.4 ºC (SE = 0.7, $n = 13$ individuals) and mean inactive T_b was 29.3 ºC (SE = 0.8, $n = 13$ individuals). A paired t-test revealed a statistically significant difference between active and inactive $T_b - T_{air}$ means ($t_{12} = 3.96$, $P < 0.001$).

Oviposition

Six different females laid eggs over the duration of the study for a total of 8 oviposition events. Both females that deposited eggs in 2009 and were radiotracked in 2010 also oviposited in 2010. Only one female radiotracked during the nesting season did not deposit eggs. Using pre- and post-oviposition body mass measurements, relative clutch mass (RCM) averaged 0.430 (mean = 0.430, SE = 0.022, $n = 7$ events). RCM was similar between years (2009: mean = 0. 411, SE = 0.067, $n = 2$; 2010: mean = 0.438, SE = 0.0235, $n = 5$) and showed no relationship with SVL ($r^2 = 0.002$, $P = 0.923$). All oviposition events took place between late-June and mid-July (Table 1.3). Females often appeared emaciated immediately after oviposition. This was characterized by parallel flaps of folded over scales running dorsal-laterally along the length of the snake's body. Two snakes (snakes D and L) were relocated in 2010 while underground in excavated

burrows actively depositing eggs. At both locations an area surrounding the burrows was enclosed with hardware cloth and monitored to confirm the presence of eggs in the ground. Hatchlings emerged between mid-August and early-September at the nests of snake D and snake L, respectively. Incubation periods were similar for both nests (53-55 and 56 days). In the earlier nest, a total of 7 hatchlings were detected over a period of 3 days from 14–16 August. In the later nest only one hatchling was detected on 01 September.

Brumation

  Specific emergence and brumation dates for individual snakes were not ascertained due to the infrequency of relocation during the early spring and fall. Some data do exist however, in the form of ranges of dates for these events (Table 1.4). Generally, snakes emerged from hibernacula sometime between mid-March and mid-April, and retreated to hibernacula in early October to early November. Snake D (a female) had both the latest (3 November 2009) and the earliest (3 April 2011) recorded active date. On 3 April 2011, three other untracked males were also found active. Snakes utilized existing mammal burrows, self-excavated burrows associated with vegetation, and old root systems for hibernacula. Of 11 total sites observed, 8 (73%) were closely associated with *P. rigida*. Three snakes were radiotracked to brumation in consecutive years. One of these snakes (snake H) used the same hibernaculum in both years. The hibernaculum consisted of a network of mammal burrows running through the root system of a stunted *P. rigida*. During the 2010 active season, the snake utilized a large area (17.8 hectare minimum convex polygon), made daily movements ranging from <1 m to ~250 m, and was as far as 466 m from the hibernaculum. In returning to the hibernaculum at the end

of the 2010 active season, the snake moved from a location 302 m away on 2 October, and was in the hibernaculum on 17 October. Of three individuals radiotracked to hibernacula in consecutive years, this was the only instance of hibernaculum site fidelity. This is believed to be the first documented record of hibernaculum site fidelity in *H. platirhinos* (Buchanan et al. *in press*). The interannual distances between hibernacula for the other two individuals were 1944 m (snake D) and 813 m (snake I). In the 11 total hibernacula observed, there were no instances of overwintering mortality.

Close Proximity Events

   There were 14 instances in which radiotracked snakes were found within close proximity ($< 5m$) to conspecifics. Ten of these encounters occurred in mid-August or later (this despite a reduced frequency of relocation in the fall months). Of these 10 events, 6 (60%) were confirmed to include snakes of both sexes (3 of the remaining 4 events involved snakes that were not captured and therefore could not be sexed). There were 2 instances (occurring in the months of June and July) in which females were found in close proximity to one another. There were also 2 instances of early-season proximity events, both occurring on 3 April 2011; one involved a radiotracked female (snake D) and an untracked male, the second involved a radiotracked male and two untracked males. Table 1.5 provides additional detail on all of these events including the individual snakes involved.

Discussion

Body Temperature and Activity

  Activity, as defined in our study, represents instances where snakes were above the surface of the substrate, not necessarily instances where snakes were not sedentary. While ambiguity is unavoidable when defining something as complex as behavior in a dichotomous fashion, the definition used was the least subjective way to define activity and provides the most useful information when considering tradeoffs between surface benefits (e.g., thermoregulation, foraging) and costs (e.g., predation risk). This scheme was selected, in part, because it was consistent with other studies of activity in *H. platirhinos* (Plummer and Mills 2010). In addition, the information gained from analyses using this definition is probably most useful for improving survey protocols. Males and females showed differences in the frequency of active behaviors; temporal differences between sexes were apparent when activity was grouped by month (Figure 1.3). Female activity was consistent throughout the months of May-August and decreased in September. With females exhibiting a substantial increase in distance moved immediately after oviposition in late-June to early-July (see Chapter 2), we may expect to see a related increase in activity. However, as the scope of our definition of "active" only reveals whether or not the snake was on the surface, the ecological nature of that activity is lost. The lack of a coincident increase in activity post-oviposition can be explained by the fact that females also showed a high degree of surface activity prior to oviposition likely related to increased thermoregulatory demands associated with egg production (i.e., basking) (Shine 2003).   Male activity appears to peak in September, coincident with an increase in average daily movements (see Chapter 2). Movements in male snakes are

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often largest during the mating season when actively pursuing females (Brito 2003, Gregory et al. 1987). Given that observations during this study confirmed a late-season breeding period, it is likely that the increase in observed male surface activity is in response to mate searching during this time of the year. Due to the infrequency of relocations during the early spring, it is possible that a second peak in activity in males, also associated with mate searching, was missed. Gibbons and Semlitsch (1987) used surface trapping to detect seasonal differences in activity in 11 terrestrial snake species in South Carolina. By quantifying trapping frequencies, they found a bimodal pattern in activity in *H. platirhinos* with peaks occurring in spring and fall, though they do not separate their data by sex.

When grouped by hours after sunrise differences in activity were apparent, but small sample sizes at the tail ends of this distribution prohibit definitive statements regarding activity during the early morning and late afternoon hours. The available data suggest that activity appears to be greatest in the morning in the 2-5 hours after sunrise. These data were further divided into a "warm season" and "cool season" based on average temperature over both years (Figure 1.2b). The results indicate partial support of the hypothesis that snakes will seek to elevate T_b (by being active on the surface) in cooler temperatures and seek to decrease T_b (by retreating beneath substrate) in warmer temperatures, though small sample sizes again limit resolution. The peak hours of activity appear to occur later in the day during the cool season compared to the warm season, suggesting that activity is delayed until later hours in the spring and fall. Moreover, in the warm season there is a gradual decrease in activity between 3-7 hours after sunrise as expected, though a spike in activity in the 7-8 hour confounds

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interpretation. We expected to see more activity in the middle of the day in the cool

season, and more activity at the tail ends of the day in the warm season. Surface activity

is predicated on a variety of influences including predation risk, foraging opportunities,

and reproductive opportunities.

  We observed notable inter-sex differences in the top-ranked mixed effects logistic

regression models assessing activity status as a function of both temporal and

microclimate predictor variables. Weighted coefficients are provided for both sexes in

Table 1.8. Because snakes are ectotherms and rely on external temperatures to raise body

temperatures that drive metabolic processes, it is not surprising that air temperature was

retained in the top-ranked models describing surface activity for both sexes. For both

sexes, a quadratic functional relationship between ambient air temperature and surface

activity better fit the data than did a standard logistic relationship. This indicates a

unimodal relationship whereby as air temperature increases, the probability of surface

activity increases to a certain point, above which the probability of surface activity begins

to decrease. The probability of activity begins to decrease in the ~20-25 ºC range (Figure

1.9). These results are consistent with a narrowing of the margin between T_b and T_{air} at

air temperatures above 22ºC (Figure 1.8), a trend that suggests behavioral avoidance of

higher temperatures in order to maintain a T_b closer to an optimal range. The most

obvious way a snake would do so would be to remove itself from exposure to solar

radiation by retreating under vegetation or leaf litter. Such behavior would result in

fewer characterizations of active behavior at higher temperatures.

  Probability of activity also increased in both sexes with greater ambient relative

humidity. Studies have demonstrated a relationship of increased anuran activity at higher

relative humidity (Bellis 1962, Oseen and Wassersug 2002). Given that amphibians are less susceptible to desiccation in humid conditions (Vitt and Caldwell 2009), anurans may increase surface activity in response to elevated relative humidity. This would increase the probability of successful foraging for *H. platirhinos*. *Anaxyrus fowleri* Hinckley (Fowler's Toad) and *Scaphiopus holbrookii* Harlan (Eastern Spadefoot Toad) account for the vast majority of prey items for *H. platirhinos* in our study area (R. Cook, US National Park Service, Wellfleet, MA, 2010 unpubl. data). While temperature and season are the predominant factors influencing surface activity in these species (Clarke 1974, Higginbotham 1939, Pearson 1955), McClean (2010) documented an increased presence of toads on humid and rainy nights in our study area.

Kitchell (1969) reported a preferred T_b of 31.76 ºC (SE = 0.32) in *H. platirhinos* in a laboratory thermal gradient. We obtained a slightly lower average T_b in our study (mean = 30.0 ºC, SE = 0.7, *n* = 13 individuals), but the greatest frequency of T_b measurements did occur in the 30-35 ºC range (Figure 1.5). T_b was significantly positively correlated with both ambient and snake level temperatures as measured at each relocation (Figure 1.7). These results are similar to findings reported from other studies (Cunnington et al. 2008, Plummer and Mills 2010), however the proportion of T_b variance explained by ambient ($r^2 = 0.613$) or snake level ($r^2 = 0.653$) temperature in our study was considerably greater than that from other studies. Plummer and Mills (2010) and Cunnington et al. (2008) report that air temperature explained 36.9% and 47.7% of *H. platirhinos* T_b variance, respectively. Reasons for the considerably higher coefficients of determination obtained in our study are unclear. In the case of Plummer and Mills (2010), higher average temperatures associated with their study area (Arkansas) may

result in proportionally more instances of avoiding higher temperatures and thus less correlation between T_b and T_{air}.

The difference between T_b in active versus inactive observations followed the expected relationship of higher T_b for active observations (mean active T_b = 30.4 ºC, mean inactive T_b = 29.3 ºC), though the modest difference between the two means (~1 ºC) makes biological interpretation difficult. Plummer and Mills (2010) showed a greater disparity between active and inactive T_b (mean active T_b = 30.5 ºC, mean inactive T_b = 27.4 ºC) among 8 *H. platirhinos* in Arkansas. We observed a clear trend of a diminishing difference between T_b and T_{air} as T_{air} increased (Figure 1.8). Given that snakes make adjustments to microhabitat selection and time of activity in order to regulate T_b (Vitt and Caldwell 2009), the observed trend indicates behavioral thermoregulation with individuals maintaining T_b within an optimal range as air temperature rises.

Reproduction

H. platirhinos breeding takes place shortly after emergence from hibernacula in the early spring and during the late summer/fall (Anderson 1965, Cunnington and Cebek 2005, Platt 1969, Plummer and Mills 1996). It is suspected that the majority of close proximity events were associated with early- and late-season courtship and copulation. We observed fewer instances of male and female snakes together in the spring than in the late summer/fall (though this may be a function of the greater relocation frequency that took place in the late summer/fall as compared to the spring). The two confirmed copulation events took place in September. In what appears to be a prolonged courtship and copulation, snake H (female) and snake O (male) were first found in contact with one another on 18 August 2010 (copulation not confirmed). On 21 August they were found

approximately 5 m from one another, both buried under leaf litter. On 25 August they were found approximately 27 m apart, both coiled and inactive. On 30 August they were again found in contact with one another, and on 7 September they were found mid-coitus. No other snakes were found in close proximity to either during this period. During this period the cumulative distance between relocations for snake H was approximately 194 m, equaling an average daily movement of 9.7 m/day. Snake O had similar movements totaling 220.7 m, for an average daily movement of 11.0 m/day. In a separate encounter involving snake I, we observed >2 snakes in contact with one another. This encounter occurred on 2 October 2009 and involved two other snakes. Unfortunately, the sex of the other two snakes was not determined. Plummer and Mills (1996) observed trailing and mating behaviors in radiotracked *H. platirhinos* in Arkansas. Their observations suggest that males trail females in the early spring and fall in an effort to copulate with them. Cunnington and Cebek (2005) observed copulation in May, August, and September in radiotracked *H. platirhinos* in Ontario. Both studies contained observations consistent with the idea that females mate with multiple males in the same season.

Egg-laying in snakes from temperate regions is often restricted to the warmest months due to the thermal requirements associated with embryogenesis (Greene 1997, Shine 2003). In our study, *H. platirhinos* oviposited during late June to mid-July and data revealed a narrow window in oviposition dates among snakes in each year. In 2009, all three females deposited eggs between 08 July and 15 July. In 2010, four out of five snakes deposited eggs between 22 June and 27 June; the fifth snake deposited eggs on 07 July. Average monthly temperatures were only slightly higher in 2010 (weather underground 2012), but 2010 represented an extreme year in terms of ground and surface

water levels. *Scaphiopus holbrookii* breeding reached unprecedented levels in 2010 (R.

Cook, US National Park Service, Wellfleet, MA, 2010 unpubl. data). These observations

are consistent with the idea that interannual variation in temperature and resource

availability has a strong influence on the timing of oviposition in snakes (Burger and

Zappalorti 1992, Shine 2003, Smith 1976). Ernst and Ernst (2003) report *H. platirhinos*

incubation periods of 39-65 days with a mean of 56 days. Our observations are

consistent with these data. In the two nests that were found and enclosed, incubation

periods were similar for both clutches (53-55 and 56 days). It is likely that more

hatchlings emerged than were detected from both nests. They may have escaped

underneath the enclosures or, in the case of the snake L nest, went undetected when the

enclosure was temporarily removed in response to impending weather (Hurricane Earl).

McCauley (1945) and Platt (1969) noted that neonates shed their skin several hours after

hatching. At the snake D nest site there were an estimated 10-15 hatchling sheds (many

in fragments) found within the enclosure suggesting that additional individuals escaped

by burrowing underneath the hardware cloth. At both sites an effort was made to retrieve

eggshells shortly after hatching, however, despite substantial effort no shells were found

at either site.

  We observed a seemingly high rate fecundity rate among females. Of 7 females

radiotracked during the nesting season, 6 deposited eggs. Moreover, a female that was

predated on 01 July 2009 was found to have well-developed eggs in her oviducts.

Finally, both females that oviposited in 2009 also oviposited in 2010. Smith (1976)

infers that reproduction does not occur on an annual basis in South Carolina based on a

small proportion of dissected mature female *H. platirhinos* found with oviducal eggs.

Greene (1997), states that *Heterodon* "produce young in alternate years or less frequently." Our observations seem to contradict these assertions and are especially surprising given that our study site was located near the northern extent of the species' range. It seems likely though, that moderate coastal temperatures that extend the activity season and an abundance of prey may explain an increased rate of reproduction of *H. platirhinos* at our study area. The results should be interpreted with caution however, as the proportion of gravid to non-gravid females in the population is unknown. The possibility does exist that the detection rate of gravid females may have been greater than non-gravid females based on the assumption that among gravid females, the heightened metabolic requirements related to egg production result in an increase in conspicuous behaviors such as basking and foraging. Future study should address this question.

Based on existing literature, it appears that there is limited knowledge of *H. platirhinos* nest site selection. Ernst and Ernst (2003) say little about *H. platirhinos* nest site selection citing only one personal observation of a nest found in a saw dust pile and Edgren (1955), who in turn, offers the following: "Natural nests are unknown for *simus* and *nasicus,* and few observations have been published on *platyrhinos*. Breckenridge (1944) reported finding two eggs at a depth of about 6 inches in a gravel deposit, and Wright and Bishop (1915) describe clutches found at depths of four to five inches in sandy fields. Cagle (1942) found a clutch under a rock." More recent accounts describe self-excavated burrows in sandy soils (Cunnington and Cebek 2005, Koch 2009). Cunnington and Cebek (2005) describe communal nesting and inter-annual fidelity among individuals to specific nest sites in Ontario, while Koch (2009) describes a high density of nest sites in Wisconsin. One could infer from these observations that adequate

nesting habitat is limiting and that there is strong selection for specific habitat features among gravid females. Cunnington and Cebek (2005) suggest the possibility that chemical cues produced by conspecifics play an important role in an individuals ability to navigate to and select nest sites. The three nest sites encountered during this study consisted of self-excavated burrows in sparsely vegetated areas with abundant loose sand and full sun exposure. All three nests were dug beneath grassy vegetation (*A. breviligulata* and/or *D. flexuousa*) suggesting that roots may have offered some stability to the structures. These results are similar to descriptions of nest sites in this species (Cunnington and Cebek 2005, Koch 2009). Burger and Zappalorti (1986) observed similar characteristics in the nest site selection of Pine Snakes (*Pituophis melanoleucus* Daudin), another sandy soil specialist, in New Jersey. While these observations are limited, based on the spatial extent and landscape composition and configuration of our study area, it is unlikely that *H. platirhinos* nesting habitat is limited. Thus, nest site fidelity and nest density may be considerably reduced in our study area compared to study areas with limited nesting habitat availability.

Seigel and Fitch (1984) list mean *H. platirhinos* RCM as 0.439. This is very similar to observations from this study (mean = 0.430, SE = 0.022, *n* = 7 events). Our data do not represent direct measurements of the eggs, rather the difference in body mass of the gravid female pre- and post-oviposition. Thus, there is some error associated with these calculations in the form of weight gained or lost between measurements that was not a direct result of oviposition (i.e., metabolism, foraging). Nonetheless, given the modest amount of time between pre- and post-oviposition weight measurements, these data are likely reasonably accurate reflections of the true RCM. While size of the individual

snake is the best predictor of clutch/litter size and clutch mass (both within and between species), RCM is generally lower in viviparous snakes compared to oviparous snakes (Seigel and Fitch 1984, Greene 1997). Among oviparous colubrids, Seigel and Fitch (1984) calculated mean RCM at 0.344 (SD = 0.087, n = 43 species), putting *H. platirhinos* towards the higher end of this RCM range. They postulate that higher RCMs should be found in cryptic or stand-and-fight species and in species that obtain prey via sit-and-wait or ambush tactics. The predatory response behavior of *H. platirhinos* is certainly consistent with this model, but the foraging mode behavior is less clear. Few data are available regarding *H. platirhinos* clutch size and reproductive rates. Future research should determine how environmental factors and resource availability influence reproductive output (Bonnet et al. 2001).

Predation and Foraging

Observations of predator and prey interactions demonstrate that *H. platirhinos* serves as an important source of energy flux within the trophic hierarchy of the ecosystems in which it is found. Two of the 16 individuals radiotracked during this study were confirmed to have been predated; one by a *C. constrictor* and the second apparently by a raptor. On Cape Cod, the ranges of *H. platirhinos* and *C. constrictor* overlap to a large degree often sharing early successional habitats. An extensive review of *C. constrictor* literature revealed three instances of predation of *H. platirhinos* by *C. constrictor*. Two of these events took place in Illinois (Hamilton and Pollack 1956, Klimstra 1959), and one took place in North Carolina (Palmer and Broswell 1995). All three accounts involved a single *H. platirhinos*. Given the extent to which *C. constrictor* diet has been studied and high degree of habitat overlap, the relatively few instances of *H. platirhinos*

predation suggest that this is a rare occurrence, perhaps because that the later tends to exist in low population densities throughout much of its range.

While *H. platirhinos* have been documented to take a variety of prey (Ernst and Ernst 2003), the dietary specialization of toads is well documented (Clark 1949, Ditmars 1907, Hamilton and Pollack 1956, Uhler and Cottam 1939). *H. platirhinos* have evolved several structural and physiological adaptations that strongly suggest a specialization for preying on toads, a group of anuran that produce potent toxins from glands located in their skin. These adaptations include enlarged posterior maxillary teeth used for securing prey and delivering a mildly toxic saliva (Kroll 1976, McAlister 1963) (but see Goodyear and Feinberg 2006), enlarged adrenal glands from which hormonal secretions serve to provide the snake with resistance to the effects of toxic toad compounds (Smith and White 1955, Spaur et al. 1971), and an elevated tongue-flicking response in the presence of anuran chemical cues (Cooper and Secor 2007). This diet specialization gives *H. platirhinos* a competitive advantage in locales with a high density of toads. *A. fowleri* and *S. holbrookii* are both common in the Province Lands section of CCNS. A lack of standardized recording precludes any formal statements, but regurgitation of *A. fowleri* during death feigning was not a rare occurrence. For example, upon initial capture in a *V. macrocarpum* dominated dune slack wetland, snake D death-feigned and regurgitated three partially digested adult *A. fowleri*. During an estimated 10-15 instances where *H. platirhinos* regurgitated prey items during death feigning, the only species observed was *A. fowleri*. This, of course, suggests that this species of toad serves as the primary prey item for *H. platirhinos* in the Province Lands. *S. holbrookii* is likely another prey item of

H. platirhinos in the study site, but the strong fossorial nature of this toad species probably limits the frequency of predation.

Despite the long-standing knowledge of *H. platirhinos* as a dietary specialist, very little information exists pertaining to foraging mode. Snake foraging behavior is often described in terms of the dichotomy of active foraging versus sit-and-wait predation, but in reality most species probably fall somewhere in the spectrum between these two extremes. Conventional theory states that slender, swiftly moving snakes tend toward the active foraging extreme, while stout bodied, slow moving snakes tend toward the sit-and-wait extreme (Greene 1997). While *H. platirhinos* certainly fall into the later physical description, the strategies by which they procure prey are poorly understood. Only one observation of a foraging event took place during this study. On 2 May 2010 at 9:05 AM, snake I was relocated and found with an *A. fowleri* in its mouth, but because the toad had already been captured by the snake at the time of relocation, very little can be inferred by the observation. What's more, the previous relocation occurred 15 days prior so little can be said about the movements (whether it was active or sedentary) of the snake just prior to the predation event. Body mass data show that *H. platirhinos* forage throughout the activity season (see Chapter 2).

Brumation

While specific brumation dates were not determined, our observations were generally consistent with those from other studies at higher latitudes showing that *H. platirhinos* emerge from brumation in March/April and retreat to hibernacula in the fall (Lagory et al. 2008, Ernst and Ernst 2003).

Pre- and post-brumation body mass measurements suggested some weight loss during brumation. Among 5 individuals radiotracked in consecutive years, 4 were lighter in the spring of the second year (mean = 14.25g lost during brumation, SE = 5.62, *n* = 4 individuals). Relative body mass lost for these snakes averaged 5.9%. One snake (snake D) was heavier (18g) suggesting late- or early-season foraging. Smith (1976) determined that fat reserves accumulated in the fall were not utilized during brumation in laboratory *H. platirhinos*. Mortality associated with brumation in temperate populations of snakes suggests that hibernacula are a limiting resource and that selection of an appropriate site is critical for survival (Mullin and Siegel 2009). The risk of mortality increases at higher latitudes and higher elevation where hibernacula must provide greater protection from freezing temperatures (Harvey and Weatherhead 2006). Hibernacula site fidelity is well documented for species that brumate communally and is thought to be, at least in part, in response to limited availability of adequate brumation habitat (Gibbons and Semlitsch 1987, Gregory 2009). For species that brumate individually (such as *H. platirhinos*), fidelity to successful overwintering sites would also seem to be advantageous, but the fact that they brumate individually may suggest that these populations have not come under the same selection pressures from habitat limitations as communally brumating snakes. Of 11 instances where we radiotracked snakes to hibernacula in the fall, all emerged in the spring. This suggests that overwintering mortality is low and that hibernacula site selection is not a critical limiting factor for *H. platirhinos* in our study area. Abundant sandy habitat and moderate coastal winter temperatures likely diminish brumation mortality for *H. platirhinos* and possibly other burrowing ectotherms on Cape Cod. The observations made during this study suggest that *H. platirhinos* undertake different

strategies when selecting a brumation site. With an abundance of apparently suitable

habitat available for hibernacula selection, we would expect site fidelity to be the

exception in this study area. Cunnington and Cebek (2005) documented interannual site

fidelity and clustering of nesting sites in *H. platirhinos* in Southern Ontario. They

postulate that because the habitat type favorable for nesting (open, sandy areas) is limited

in their study area, *H. platirhinos* nest in high densities in these areas. These

observations are consistent with the idea that availability of certain habitat features is a

factor in determining the frequency of fidelity to sites used for essential life cycle events.

Another observation made on 4 April 2011 confounds this argument however, as it

hints at a potential instance of communal use of hibernacula in our study area. Two

untracked male *H. platirhinos* were found coiled above ground within 5 m of a

radiotracked male that remained underground in the root system of a stand of stunted *P.*

rigida. Assuming these two snakes had recently emerged from the same root network as

the individual that remained underground, this would suggest aggregation during

brumation. Of course, it is impossible to say if these two individuals emerged from the

same location or had recently traveled to it (though the former is suspected). Regardless,

given this possible instance of communal brumation as well as our single confirmed

documentation of hibernaculum site fidelity (believed to be the first occurrence ever

documented for this species), it is apparent that there are still considerable knowledge

gaps in the realm of brumation ecology in *H. platirhinos*.

Scope and Limitations

Several factors limit the interpretive power of the data collected. A limited sample size

of individuals reduces statistical power of analyses that attempt to gauge spatial, and

temporal influence on physiological data (T_b) and behavior and increases the likelihood that a non-representative individual could skew data. The frequency of relocation of snakes was selected as an attempt to balance the collection of enough data to accurately reflect *H. platirhinos* response to its environment (presumed to increase with greater frequency) and disturbance to individuals as a result of tracking and handling (presumed to decrease with reduced frequency). Moreover, because autocorrelation is often an issue when studying the movements of reptiles, it was deemed important to give ample time between relocations to prevent a lack of independence between points (White and Garrott 1990). Some variation in the frequency of relocation occurred as a result of an ability to find snakes and other logistical constraints. Thus, resolution is lost for portions of the activity season where frequency of relocation was not adequate. The periods of the year most significantly affected were during the early spring (late March-April) and the late fall (November).

Formal characterization of snake activity was not adopted until several weeks into the project. Thus, activity data was lost for a significant number of relocations ($n = 59$). This reduced the sample size and statistical power of tests dealing with activity.

One cannot ignore the fact that surgically implanting a radio transmitter into the body cavity of a snake probably comes at some cost to the snake. While it is impossible to say without formal experimentation what influence this has on a given species of snake and their ability to behave normally, there is some evidence that radio transmitter implantation in snakes does elicit a hematological response (Lentini et al. 2011) and has an effect on growth, reproduction, and survival (Weatherhead and Blouin-Demers 2004) in certain species. Whether or not this changes the way in which results from

radiotelemetry should be interpreted is another question. Assuming that the expected

impact to a snake would reduce the number of movements and the distances moved

(Fitch and Shirer 1971), one might expect that the measurements of activity range (i.e.,

home range) and daily movements are underestimates. In this study there was no obvious

direct impact to any individual's ability to move, find prey, or reproduce successfully. Of

16 snakes radiotracked, 8 were confirmed alive at the conclusion of the study. Of 7

females radiotracked during the season in which oviposition takes place, 6 deposited

eggs. Two of these females laid eggs in consecutive years. All individuals radiotracked

for an extended period of time demonstrated an ability to forage successfully (see

Chapter 2). Certainly, more studies like the ones cited above that investigate impacts of

radio telemetry on snakes are warranted.

Instances of signal loss remain something of a mystery. In addition to the instance of

snake M (as detailed in the Results), there were three other instances where signal was

lost for a substantial period of time (14-22 days) only to have snakes relocated in

locations within range of the receiver from their previous relocation. It is difficult to say

whether these prolonged absences were the result of signal loss associated with

transmitter problems, topography and vegetation, or with long-distance unidirectional

movements and subsequent returns. If the last, an increased frequency of relocation

would probably serve to reduce the likelihood of this occurring in future studies.

Expulsion of foreign objects (including radiotransmitters) from the body cavity has

been documented in snakes via absorption by the gastrointestinal tract (Pearson and Shine

2002, Roark and Dorcas 2000). Tracy et al. (2011) documented absorption of foreign

objects by the bladder in amphibians. It is unlikely however, that the instance where only

a transmitter was found (snake E) occurred as a result of internal absorption and subsequent expulsion given the short amount of time post-surgery that the event took place. There is some anecdotal evidence that *H. platirhinos* can actively expel foreign objects through the skin (J. Feinberg, Rutgers University, New Brunswick, NJ, 2011 pers. comm.). The phenomenon is poorly understood among most species and warrants further study to ascertain the likelihood of such an event. Also worth studying would be whether the methods of expulsion are consistent (or diverge) along phylogenetic lines.

Conclusions

Throughout its range, *H. platirhinos* appears to be most vulnerable to extirpation in southern Canada and the northeastern United States. Fundamental biological information is essential to the success of conservation programs and will help focus management efforts. Body temperature results, activity season range, and the timing of mating and oviposition were consistent with other studies. Fecundity rates were higher in our study than those from other studiesof *H. platirhinos*. There were differences in the factors influencing male and female activity, though relative humidity emerged as the primary factor for both sexes. Hibernacula do not appear to be limiting at our study site, though we did document the first observed record of hibernacula site fidelity. This study should enhance the understanding of fundamental aspects of *H. platirhinos* ecology in this part of its range. Our results will also help to enhance future survey protocols for this cryptic and notoriously hard to detect species.

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Table 1.1. Summary of telemetered *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Snake ID	Sex	Weight (g)	SVL (mm)	TL (mm)	Range of dates radiotracked	Duration of dates radiotracked	Number of relocations	Fate
A	M	146	540	585	051109-051909	8	3	Signal lost
B	F	323	740	880	051209-070109	50	18	Predated (bird?)
C	F	161	500	595	051609-053109	15	7	Eaten by black racer
D	F	400	685	820	051609-112010	553	66	Underground on 11/20/10
E	F	273	650	782	052209-052309	1	1	Found only transmitter
F	F	232	580	694	053009-071109	42	14	Died laying eggs
G	M	139	465	580	061309-052510	346	34	Signal lost
H	F	325	610	745	061309-101710	491	59	Underground on 10/17/10
I	M	246	531	678	072709-101710	447	48	Underground on 10/17/10
J	F	200	565	670	081209-091710	401	41	Signal lost
K	F	632	780	947	060410-101710	135	24	Above ground on 10/17/10
L	F	239	585	698	060410-101610	134	26	Above ground on 10/16/10
M	M	128	500	580	060410-082610	83	20	Signal lost
N	F	198	520	625	061810-102210	126	20	Underground on 10/16/10
O	M	336	635	817	062610-101710	113	14	Above ground on 10/17/10
P	M	178	484	609	062610-102210	118	18	Underground on 10/16/10
Female Total	-	-	-	-	-	1948	276	-
Male Total	-	-	-	-	-	1115	137	-
Total	-	-	-	-	-	3063	413	-
Female Mean	-	298.3	621.5	745.6	-	194.8	27.6	-
(SE)	-	(48.5)	(28.8)	(35.9)	-	(65.4)	(6.8)	-
Male Mean	-	195.5	525.8	641.5	-	185.8	22.8	-
(SE)	-	(33.1)	(24.7)	(38.3)	-	(69.8)	(6.5)	-
Total Mean	-	259.8	585.6	706.6	-	191.4	25.8	-
(SE)	-	(31.8)	(23.1)	(28.7)	-	(47.0)	(4.8)	-

Table 1.2. Body temperature data (ºC) for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Snake	Range T_b	Mean T_b (All observations)	SE	N	Mean T_b (Activity season only)	SE	N
A							
B	12.5-37	25.0	2.12	12	25.0	2.12	12
C							
D	6.5-37	26.7	1.05	54	27.5	0.93	52
E							
F	17.5-34.5	28.4	1.65	12	28.4	1.64	12
G	15-35	27.4	1.19	33	28.5	1.12	30
H	5.5-36	28.6	0.97	57	29.3	0.86	55
I	7-35.5	28.3	0.98	47	29.4	0.80	44
J	7-36	28.4	1.27	39	29.4	1.13	37
K	30-36	33.4	0.42	21	33.4	0.42	21
L	18-34.5	30.3	0.82	22	30.3	0.81	22
M	25.5-36	32.5	0.57	18	32.5	0.57	18
N	18-35.5	30.6	1.20	18	32.2	0.64	16
O	28-39.5	33.0	0.68	14	33.0	0.67	14
P	15.5-33	29.9	1.05	16	31.2	0.34	14
Female	5.5 - 37	28.9	0.90	8	29.4	0.92	8
Male	7 - 39.5	30.2	1.11	5	30.9	0.86	5
All snakes	5.5 - 39.5	29.4	0.69	13	30.0	0.67	13

Table 1.3. Summary of telemetered *H. platirhinos* oviposition data from Cape Cod National Seashore 2009-2010.

Snake	Year	Pre-oviposition body mass (g)	Post-oviposition body mass (g)	Difference (g)	RCM (%)	Possible oviposition dates	Hatch dates	Number of hatchlings detected	Incubation period (days)
D	2009	370	193	177	47.8	0708-0712	-	-	-
H	2009	308	202	106	34.4	0711-0715	-	-	-
F	2009	-	-	-	-	0711[a]	-	-	-
D	2010	415	237	178	42.9	0622[a]	0814-0816	7?	53-55
H	2010	382	238	144	37.7	0622-0624	-	-	-
K	2010	541	299	242	44.7	0622-0624	-	-	-
L	2010	245	143	102	41.6	0707[a]	0901	2	56
N	2010	198	95	103	52.0	0622-0627	-	-	-
Mean	-	-	-	150.3	43.0	-	-	-	-
(SE)	-	-	-	(19.8)	(2.2)	-	-	-	-

[a] Denotes that snake was found actively depositing eggs.

Table 1.4. Emergence and brumation dates for telemetered *H. platirhinos* at Cape Cod National Seashore 2009-2011.

Snake	Sex	Year	Possible emergence date	Possible initial brumation date	Hibernaculum description
D	F	2009	-	Post 1103	Underground near base of pitch pine tree
D	F	2010	0316-0418	1017-1120	Self-dug burrow in open sand/ground level veg
D	F	2011	0314-0403	-	-
G	M	2009	-	1008-1021	Mammal burrows under pitch pine
G	M	2010	0316-0418	-	-
H	F	2009	-	1009-1105	Root system/mammal burrows beneath scrubby pitch pine
H	F	2010	0316-0418	1002-1017	Root system/mammal burrows beneath scrubby pitch pine
H	F	2011	Post 0403	-	-
I	M	2009	-	1009-1015	Self-dug burrow in open sand/ground level veg
I	M	2010	0316-0418	1002-1017	-
J	F	2009	-	1023-1103	Underground beneath scrubby pitch pine
J	F	2010	0316-0418	-	-
K	F	2010	-	Post 1017	Underground beneath lichen on side of north-facing hill
K	F	2011	Post 0403	-	-
L	F	2010	-	Post 1016	Mammal burrows under pitch pine
L	F	2011	Post 0403	-	-
N	F	2010	-	1002-1016	Underground beneath pine needles
N	F	2011	Post 0403	-	-
O	M	2010	-	Post 1017	Underground beneath pine needles
O	M	2011	Post 0403	-	-
P	M	2010	-	1002-1016	Burrowed beneath large pitch pine branch
P	M	2011	0314-0403	-	-

Table 1.5. Summary of close proximity events (<5m) of *H. platirhinos* at Cape Cod National Seashore 2009-2011.

Date of encounter	Time	Radiotracked snake(s) involved	Sex	Other snake(s) involved	Coitus[a]	Description of event
9/18/2009	11:09	H	F	New unknown sex	S	New snake was coiled on top of Snake H; not captured
10/2/2009	12:35	I	M	2 New unknown sex	S	Snake I coiled with 2 other snakes; not captured
6/6/2010	17:10	J	F	Snake N (female)		Snake N found moving through grass ~1m from Juliet
7/28/2010	8:58	N	F	New female		New snake found ~2m from Snake N; both coiled
8/18/2010	13:00	H,O	F, M	-	S	Snakes found together (recent shedding by Snake H)
8/18/2010	15:45	N	F	Unknown sex	S	Snake N in contact with new snake; not captured
8/21/2010	15:37	H,O	F, M	-		Both snakes buried in litter ~5m from one another
8/30/2010	12:15	H,O	F, M	-	S	Both snakes in same overhanging burrow at edge of marsh
8/30/2010	13:00	K	F	New male	S	New snake found coiled atop leaf litter ~1m from Snake K
9/7/2010	14:10	H,O	F, M	-	O	Observed mid-coitus
9/17/2010	14:50	J	F	New male	O	New snake found mid-coitus with Snake J
10/2/2010	14:19	P	M	New male		New snake found moving ~3m from Snake P
4/3/2011	9:25	D	F	New male	S	New snake found active <1m from Snake D
4/3/2011	13:56	O	M	2 New males		New snakes found w/in 2m of Snake O hibernaculum

[a]S denotes suspected recent copulation,
O denotes observed
copulation

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Table 1.6. Variables used in mixed effects logistic regression activity analysis for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Variable	Description
hours.post.sunrise + hours.post.sunrise^2	Quadratic term for time of relocation adjusted for hours after sunrise; scaled continuosly[a]
hours.post.sunrise	Time of relocation adjusted for hours after sunrise; scaled continuously[b]
amb.temp + amb.temp^2	Quadratic term for air temperature measured 1m above snake location[c]
amb.humid	Relative humidity measured 1m above snake location[c]
avg.wind	30 second wind speed average measured 1m above snake location[c]
julian	Date of relocation according to Julian calendar[c]

[a] used in female models only

[b] used in male models only

[c] used in male and female models

Table 1.7a. Mixed effects logistic regression modeling results for female activity of *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Rank	Model	k	AIC_c	ΔAIC_c	ω
1	amb.humid + hours.post.sunrise + hours.post.sunrise^2 + amb.temp + amb.temp^2	5	260.69	0.00	0.68
2	amb.humid + amb.temp + amb.temp^2 + julian + hours.post.sunrise + hours.post.sunrise^2	6	262.80	2.11	0.24
3	amb.humid + amb.temp + amb.temp^2	3	265.72	5.03	0.06
4	julian + amb.humid + amb.temp + amb.temp^2	4	267.84	7.15	0.02
5	amb.temp + amb.temp^2 + hours.post.sunrise + hours.post.sunrise^2	4	272.57	11.88	0.00
6	hours.post.sunrise + hours.post.sunrise^2 + amb.humid	3	273.71	13.03	0.00
7	amb.temp + amb.temp^2 + hours.post.sunrise + hours.post.sunrise^2 + julian	5	274.46	13.77	0.00
8	julian + hours.post.sunrise + hours.post.sunrise^2 + amb.humid	4	274.80	14.11	0.00
9	amb.humid	1	276.05	15.36	0.00
10	amb.humid + julian	2	277.56	16.87	0.00

Table 1.7b. Mixed effects logistic regression modeling results for male activity of *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Rank	Model	k	AIC_c	ΔAIC_c	ω
1	amb.humid + amb.temp + amb.temp^2	3	120.11	0.00	0.39
2	julian + amb.humid + amb.temp + amb.temp^2	4	122.10	1.99	0.14
3	amb.humid + hours.post.sunrise + amb.temp + amb.temp^2	4	122.26	2.15	0.13
4	amb.temp + amb.temp^2	2	122.38	2.27	0.12
5	amb.temp + amb.temp^2 + hours.post.sunrise	3	123.31	3.20	0.08
6	amb.temp + amb.temp^2 + julian	3	123.92	3.82	0.06
7	amb.humid + amb.temp + amb.temp^2 + julian + hours.post.sunrise	5	124.40	4.29	0.05
8	amb.temp + amb.temp^2 + hours.post.sunrise + julian	4	125.45	5.34	0.03
9	amb.humid	1	131.55	11.44	0.00
10	amb.humid + julian	2	131.81	11.70	0.00

AIC_c = second-order Akaike's Information Criteria (for small sample sizes), k = number of parameters, ω_i = relative amount of support for the model

Table 1.8. Weighted coefficients for activity analysis for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

	Variable	Coefficient	Odds Ratio
Males	*amb.humid*	0.021	1.021
	amb.temp	1.043	2.837
	amb.temp^2	-0.026	0.975
	julian	0.003	1.003
	hours.post.sunrise	-0.061	0.941
Females	*amb.humid*	0.029	1.030
	hours.post.sunrise	0.804	2.234
	hours.post.sunrise^2	-0.060	0.942
	amb.temp	0.276	1.318
	amb.temp^2	-0.005	0.995
	julian	-0.001	0.999
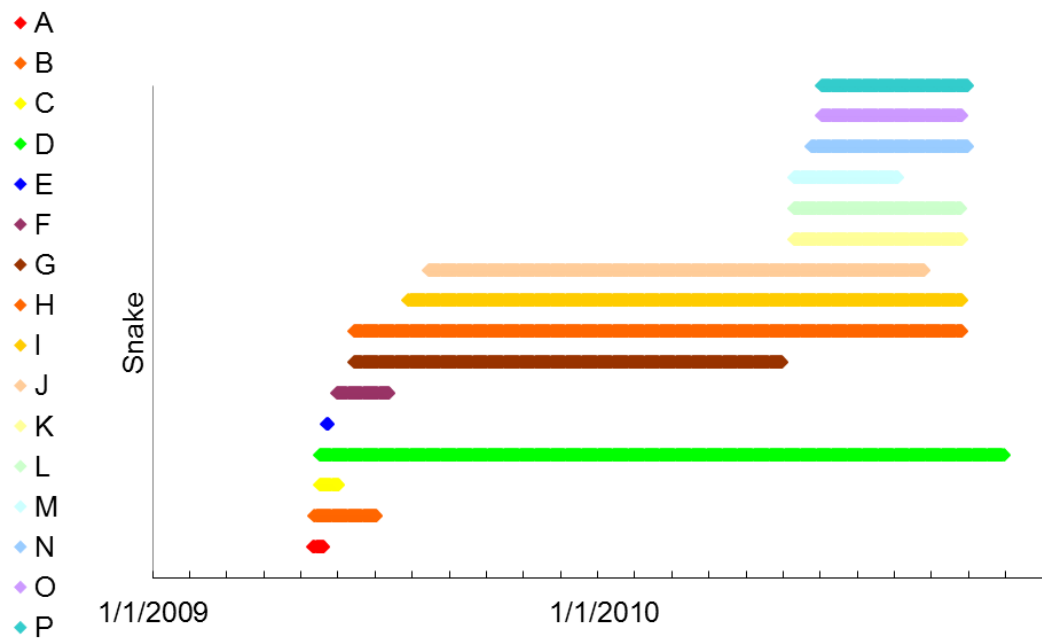
Figure 1.1. Diagram illustrating the duration of tracking for each *H. platirhinos* monitored at Cape Cod National Seashore 2009-2010. Each tick mark on the x-axis represents a 30 day period.

Figure 1.2a
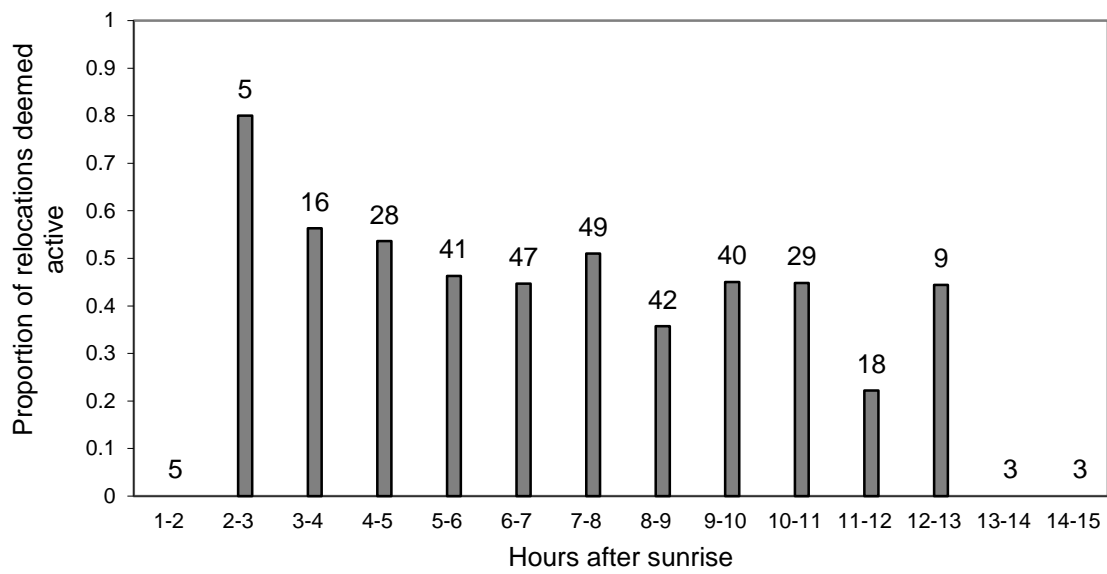
Figure 1.2b.
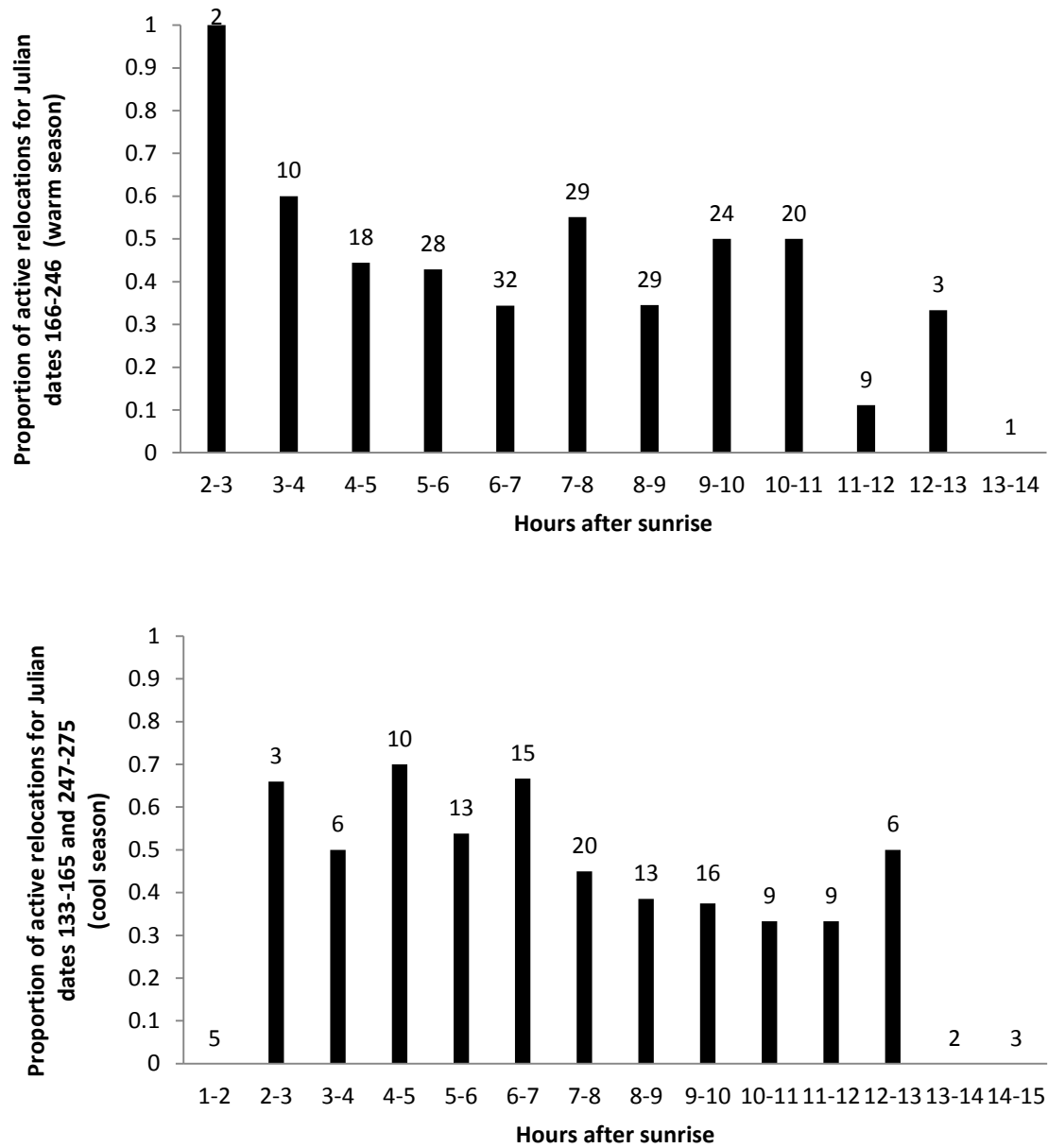
Figure 1.2. Proportion of active relocations grouped by hours after sunrise (sexes combined) for *H. platirhinos* at Cape Cod National Seashore 2009-2010. Numbers above bars indicate sample sizes. a. All observations combined. b. The top graph shows all relocations for June 19 – August 30 in both years. The bottom graph shows all relocations for May 13 – June 18 and August 31 – October 2 in both years.
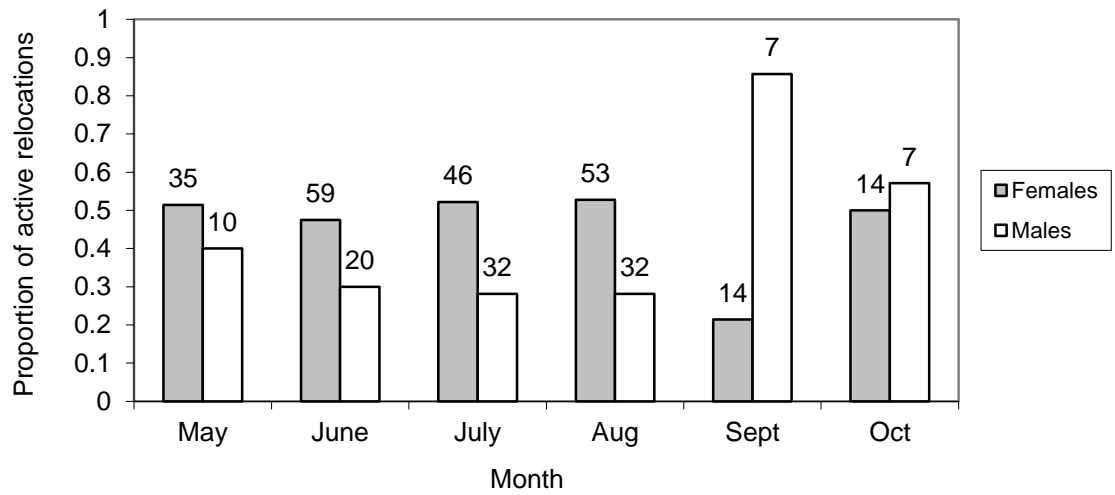
Figure 1.3. Proportion of active relocations grouped by month for *H. platirhinos* at Cape Cod National Seashore 2009-2010. Numbers above bars indicate sample sizes. Months with sample sizes less than 7 were excluded from analysis (April and November).
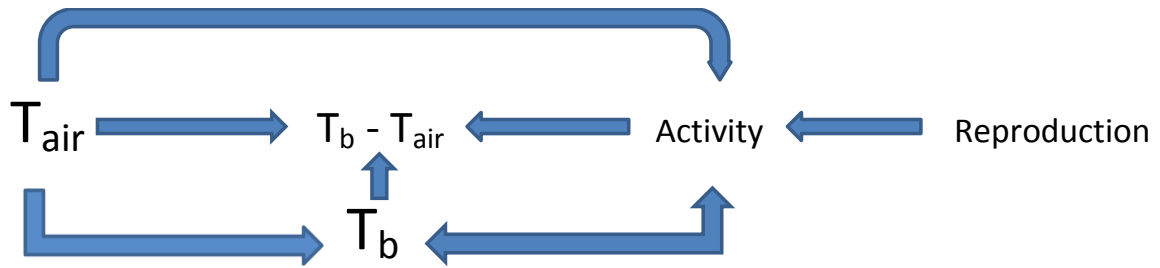
Figure 1.4. Conceptual model showing the relationships between ambient air temperature (T_{air}), body temperature (T_b), and behavior.
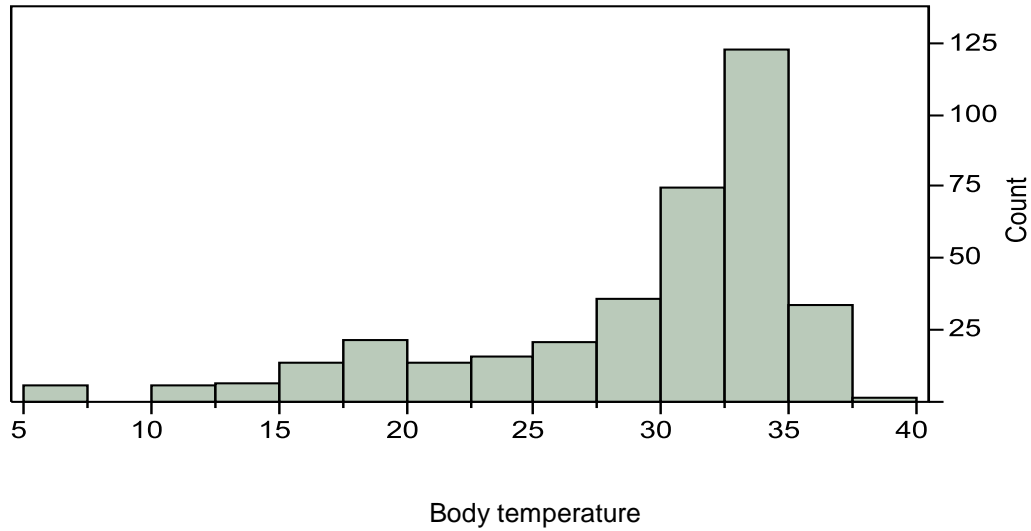
Figure 1.5. Distribution of body temperatures (ºC) (*n* = 363) of *H. platirhinos* at Cape Cod National Seashore 2009-2010.
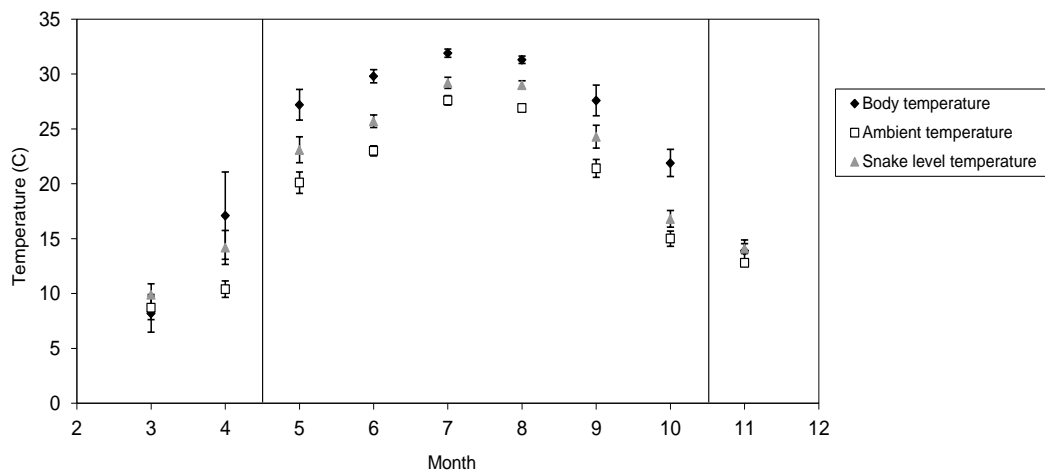
Figure 1.6. Mean body temperatures, mean ambient temperatures, and mean snake level temperatures by month for relocations of *H. platirhinos* at Cape Cod National Seashore 2009-2010. Error bars represent +/- one SE. Vertical bars represent an approximation of the activity range for the species at this study site.
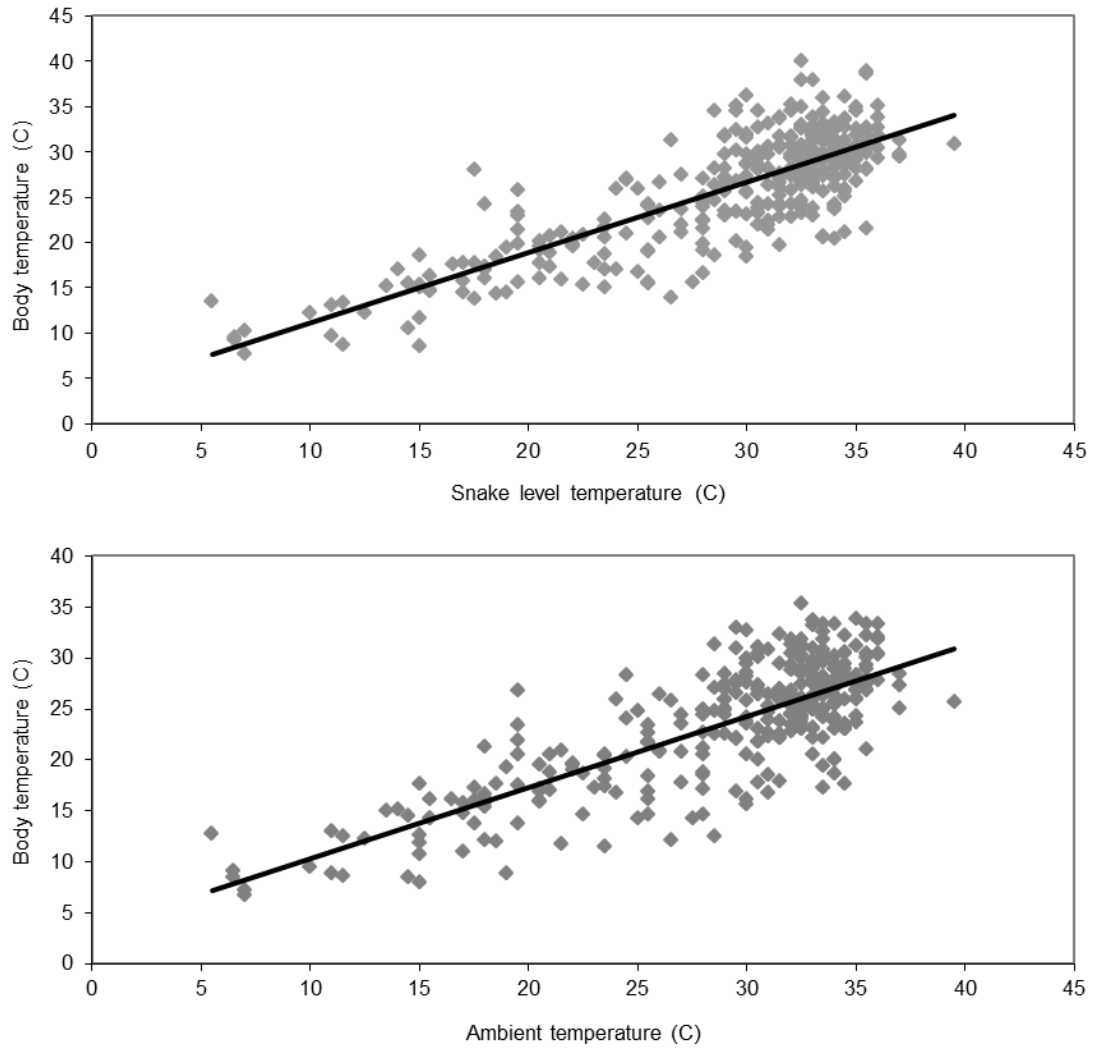
Figure 1.7. Linear regression of body temperature over snake level temperature (r^2 = 0.6527, $P < 0.001$, slope = 0.84) and ambient temperature (r^2 = 0.6127, $P < 0.001$, slope = 0.88) for *H. platirhinos* at Cape Cod National Seashore 2009-2010. Quadratic regression (not shown) explained more of the variation in T_b (ambient r^2 = 0.679, $P < 0.001$; snake level r^2 = 0.737, $P < 0.001$).
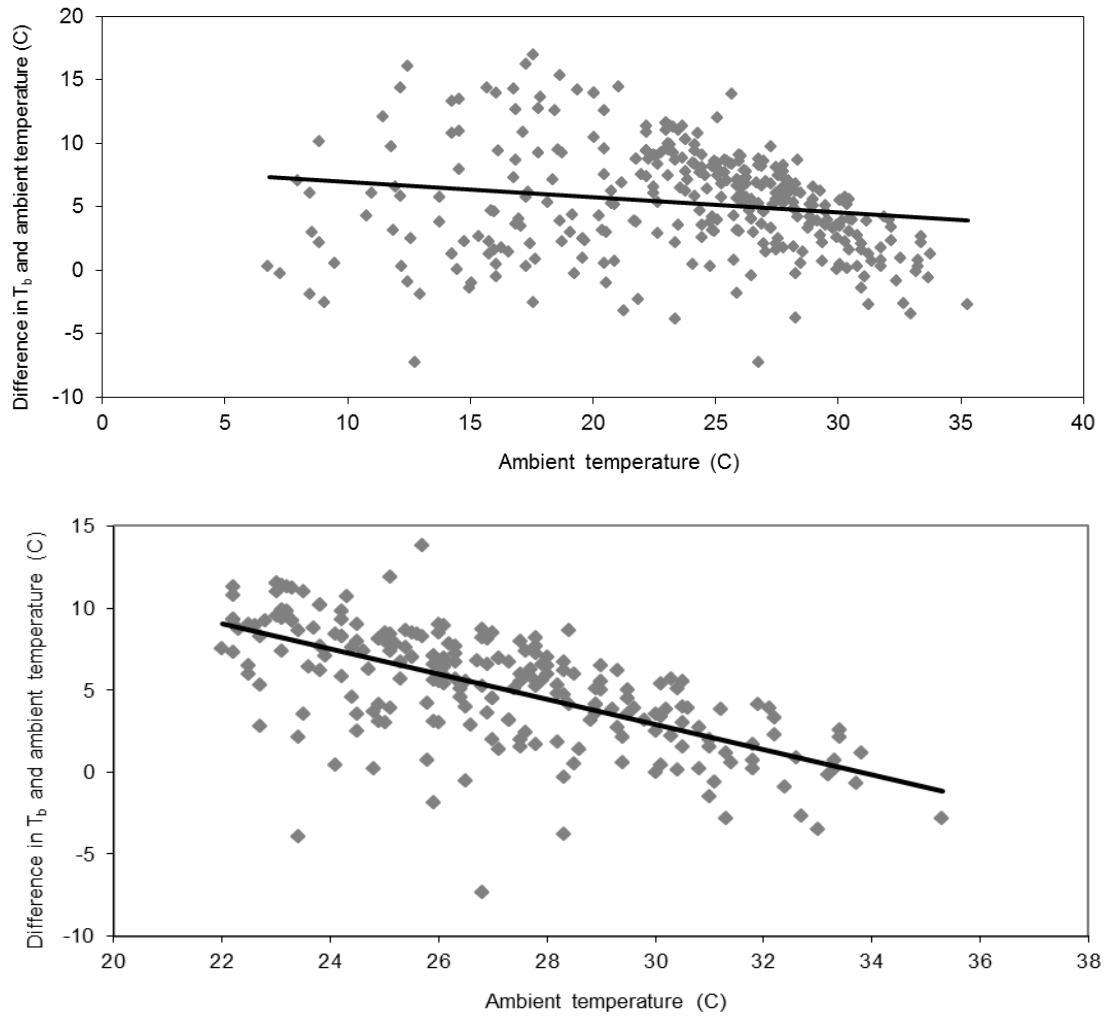
Figure 1.8. Linear regression of difference in T_b and T_{air} over T_{air} ($r^2 = 0.029$, $P = 0.0016$, slope = -0.12) for *H. platirhinos* at Cape Cod National Seashore 2009-2010. The bottom graph is a subset of the top graph (of temperatures >22 ℃) which shows the narrowing of the difference between T_b and T_{air} as ambient temperature increases ($r^2 = 0.424$, $P < 0.001$, slope = -0.77).
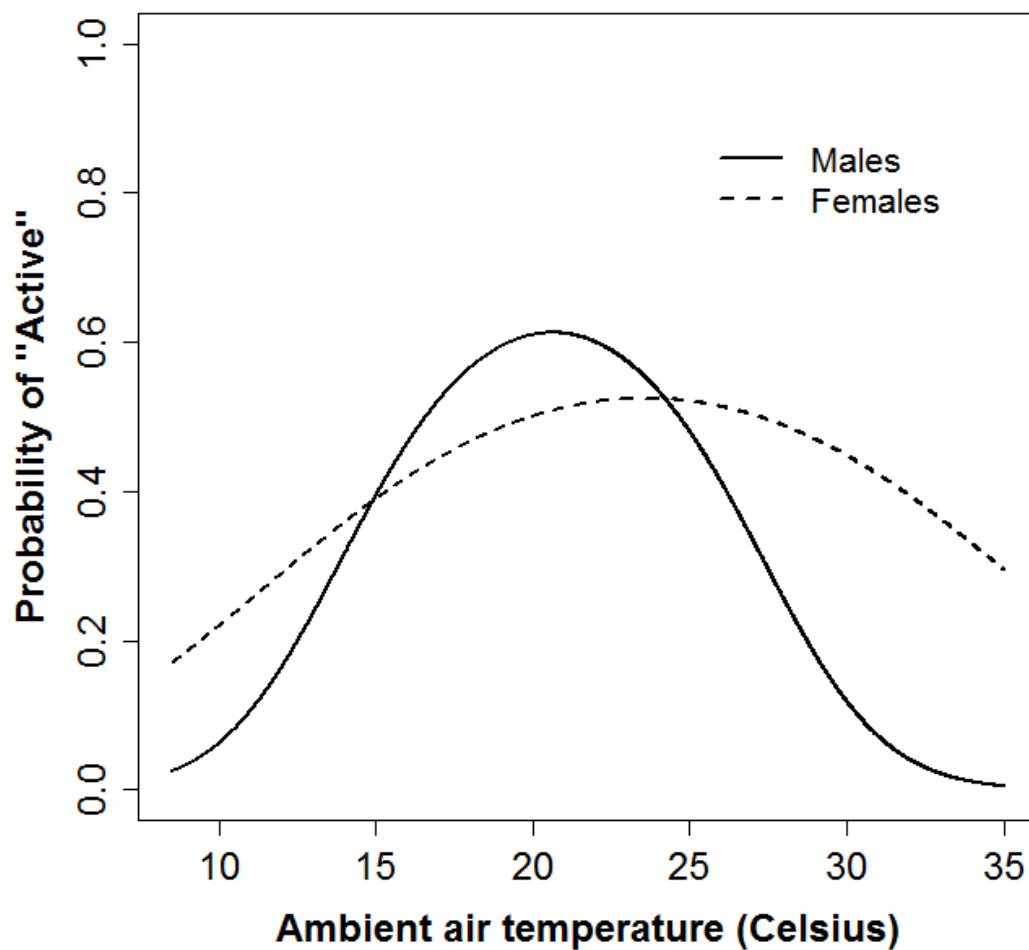
Figure 1.9. Results from mixed effects logistic regression showing the unimodal relationship in air temperature and probability of active behavior for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

CHAPTER 2

SPATIAL ECOLOGY AND HABITAT SELECTION OF THE EASTERN HOGNOSE

SNAKE (*HETERODON PLATIRHINOS*) AT CAPE COD NATIONAL SEASHORE,

BARNSTABLE COUNTY, MASSACHUSETTS

Introduction

Movements and selection of habitat represent fundamental information when attempting

to understand the ways in which a species interacts with its environment. These

processes are inextricably related in that they are both responses to life's most pressing

requirements. Spatial movements are predominantly a response to an individual's need

for food resources, reproductive partners, and other essential aspects of reproduction and

survival (e.g., nest sites, adequate hibernacula), while the use of certain physical and

vegetative features as an organism navigates through its environment represents habitat

selection. Radiotelemetry is an effective way of studying these processes in wildlife

populations, especially in species that are cryptic and difficult to detect, like most snakes

(Keller and Heske 2000, Moore and Gillingham 2006, Reinert 1984a). By monitoring

individuals over extended periods of time, we gain a better understanding of the causative

factors behind the spatial and temporal distribution of organisms throughout their

geographic range (Durner and Gates 1993, Harvey and Weatherhead 2006, Sperry and

Weatherhead 2009). Spatial ecology and habitat selection represent fundamental

ecological information that is necessary for successful implementation of conservation

and management programs (Shine and Bonnet 2009).

Heterodon platirhinos Latreille (Eastern Hognose Snake) is a species of increasing

conservation concern, especially in the northeastern United States (Klemens 1993,

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NEPARC 2010, Seburn 2009, Therres 1999). Noted declines are believed to be the result of direct anthropogenic pressures including habitat loss and fragmentation, road mortality, environmental degradation, and indiscriminate killing (Ernst and Ernst 2003, Gibbons et al. 2000). Very few studies have compiled quantitative spatial ecology and habitat information for single populations of this species over multiple years. Probably contributing to this dearth of information is the species' cryptic nature and the fact that throughout most of its range *H. platirhinos* appears to occur in low population densities relative to sympatric snake species (Fitch 1993, Ford 1991). Among the variety of habitat types in which *H. platirhinos* is found, the snake occurs in greatest densities in well drained, sandy soils (Conant 1938, Fitch 1993). Barrier beach and dune ecosystems appear to contain the highest densities of the species due to abundant prey (primarily toads) and expanded niche opportunity as a result of reduced snake fauna (Brady 1925, Scott 1985, Stewart and Rossi 1981). The northern tip of the Cape Cod peninsula consists of an expansive, early successional sand dune landscape known to contain a robust population of *H. platirhinos*. A radiotelemetry study was carried out from May 2009 to March 2011 to assess spatial use and habitat selection of *H. platirhinos* in this section of Cape Cod National Seashore.

Materials and Methods

Study Area

Cape Cod National Seashore (CCNS) is located in Barnstable County in southeastern Massachusetts. Cape Cod is a long, narrow peninsula that extends out into the Atlantic Ocean (Figure 2.1). The study was conducted at the outermost portion (northern

terminus) of the peninsula in an approximately 1,800 hectare section of the park known as the Province Lands. Whereas the rest of Cape Cod consists of large quantities of sand, silt, and clay left behind by Pleistocene glaciers, the Province Lands consist entirely of postglacial deposits of eroded coastal sediments carried north by long-shore currents. Over time, predominant marine and aeolian forces have given the hook-like tip of the peninsula its distinctive spiral shape and formed the parabolic dune landscape that exists there today (Uchupi et al. 1996). Soils in the Province Lands consist almost entirely of sand. Elevations range from approximately 0 to 33 meters above sea level. Intensive land use by European settlers, which included clearing of forest for fuel and grazing, and the prevalent xeric conditions have resulted in a patchy mosaic of early successional communities including open dune soil crusts, heathland-like assemblages, dune grasslands, shrubs, and scrub woodlands. Upland forest types are dominated by *Pinus rigida,* with some *Quercus velutina,* and *Q. ilicifolia.* Dune grasslands are dominated by *Ammophila breviligulata* and *Deschampsia flexuousa.* Heathland-like communities consist of mats of colonizing lichens, dwarf shrubs, and *Toxicodendron radicans*. The grasslands and heathlands are often interspersed with single shrubs or mixed shrub patches of *Prunus maritima*, *Prunus serotina*, *Morella pensylvanica, and Rosa rugosa*. Dune slack wetlands occur where wind-scour has lowered the surface elevation to where it seasonally intersects the groundwater table. These wetlands are relatively diverse systems, but the most abundant species include *Vaccinium macrocarpum*, *Morella pensylvanica*, *Kalmia angustifolia*, *V. corymbosum*, and *Juncus greenei* (Smith et al. 2008). Tidally influenced salt marshes occupy portions of the land-sea interface.

Radiotelemetry

Individual *H. platirhinos* were located by active searches, incidental encounters by park staff, and in proximity to other radiotracked snakes. Radio transmitters included models SI-2T 11g, SI-2T 9g, and SB-T 5g produced by Holohil Systems Ltd (Carp, Ontario, Canada). Implantation surgeries were performed using techniques modified from Reinert and Cundall (1982), as detailed in Calle et al. (2005). Transmitters did not exceed 4.5% of snake body mass (mean = 3.2% , SE = 0.29, *n* = 16 individuals). All snakes were held in post-operative veterinary quarantine for a minimum of 24 hours until they exhibited signs of full recovery. There was no mortality associated with surgery. Following release at their original points of capture, snakes were radiotracked using a Telonics TR-4 radio receiver (Telonics Inc., Mesa, AZ) and a three-point Yagi antenna. Multiple studies have indicated that *H. platirhinos* are predominantly diurnal (Platt 1969, Plummer and Mills 2000). Thus, all relocations occurred during daylight hours only.

Data Collection

At each snake relocation data were collected on body temperature and geographic location. In addition, body mass was measured to the nearest 1g approximately once every two weeks using a Pesola^{TM} spring scale. Body temperature (to the nearest 0.5º C) was determined by measuring the pulse interval of the temperature-sensitive transmitters. A pulse interval was obtained by timing the length (in seconds) between ten pulses and calculating an average. This value was applied to a pre-calibrated curve provided by the transmitter manufacturer to obtain T_b. Geographic location was recorded in Universal Transverse Mercator (UTM) coordinates (North American Datum of 1983) using a

Garmin GPS 72 handheld global positioning system receiver (Garmin International Inc., Olathe, KS) with accuracy of ~3m.

A suite of physical and vegetative habitat characteristics deemed potentially meaningful were collected at a subset of snake locations (hereafter "use") and paired random locations (Table 2.1). Paired random locations were intended to represent available habitat and were determined by randomly generating a compass direction (0-359º) and a distance between 1 and 150 m from the use location. A compass was used to determine the azimuth and distance was determined using a range finder and/or pacing. In order to assess *H. platirhinos* habitat selection at multiple spatial scales, data were collected within a 1m² quadrat centered on the snake location, and within a 15 m radius circle of this point divided into 4 quarters. Each quarter was sampled using a 4 m by 4 m quadrat placed randomly using a generated distance (1-15m) and direction (0-89º, 90-179º, 180-269º, and 270-359º). All coverage estimates and measurements were collected in each 4 m by 4 m quadrat and means were taken for each variable to be used in analysis. For continuity between plots, each corner of the 1m² quadrat was aligned to a cardinal direction. Divisions between quarters in the 15 m radius circle plot were also aligned to cardinal directions (Figure 2.2). Identical data collection took place at each paired random location.

Statistical Analysis

Reptiles often exhibit strong differences in activity and use of habitat between intraspecific reproductive classes (Millar and Blouin-Demers 2011, Reinert 1984b, Wund et al. 2007). In radiotelemetry studies, females are often subdivided into gravid and non-gravid classes. Due to a limited number of radiotracked non-gravid females ($n = 2$)

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however, no subdivision was carried out; all females in this study were considered as one class.

Distances between relocations were converted to average daily movements (ADMs) by dividing each calculated distance between sequential relocations by the number of days elapsed. This created a distribution of distances allowing for the calculation of means and variance where appropriate (Diffendorfer et al. 2005) (Table 2.2). Only observations collected during the months of May-October were considered for ADM analyses due to reduced frequency of relocation in the early spring and late fall. ADMs were heavily skewed and did not meet assumptions of normality (Figure 2.3). Therefore, nonparametric Wilcoxon tests were used to assess differences between sexes. To avoid pseudoreplication and inflating degrees of freedom for statistical tests (White and Garrott 1990), the overall difference between sexes was tested using ADM means for each individual for all observations, while monthly differences between sexes were tested using ADM monthly means (different for each year) for each individual.

Estimates of home range were calculated using minimum convex polygons (MCPs) (Table 2.3, Figure 2.4) and fixed kernel density estimates (KDEs). Least-squares cross-validation (LSCVh) is the most common method of determining a smoothing factor for KDE analysis (Seaman and Powell 1996), especially when estimating core use (Blundell et al. 2001). However, due to small sample size and the resultant under-smoothed density estimates that were difficult to interpret when calculated using LSCVh, likelihood cross-validation (CVh) was selected as a more appropriate smoothing factor for KDEs in our study (Horne and Garton 2006). Though single wayward movements can significantly inflate polygon size, MCPs are simple and do not rely on an underlying statistical

distribution to estimate home range size (Row and Blouin-Demers 2006). Moreover, MCPs are widely used in home range analysis of snakes (Lagory et al. 2009, Plummer and Mills 2000, Row et al. 2012) making them the most useful for comparison with other studies. Nonparametric Wilcoxon tests were used to assess differences between sexes in home range estimates as they did not meet assumptions of normality. To examine inter-annual difference in size and location of home range, annual MCPs and core areas (50% KDEs) were calculated for three snakes that were radiotracked in 2009 and 2010 throughout the majority of the activity season in both years. Percent overlap of annual MCPs and core areas were calculated for these individuals by dividing the total area of overlap of the 2010 polygon by the total area of the 2009 polygon (Table 2.4). Linear regression was used to assess the relationship between home range size (MCP and KDE) and both number of relocations and snout-vent-length (SVL). Only snakes with 14 relocations or greater ($n = 13$) were considered in home range analyses; a number of relocations comparable to other studies of home range on *H. platirhinos* (Lagory et al. 2009).

Paired logistic regression, a method somewhat analogous (in terms of use) to a paired *t*-test, was used to assess differences between snake use and paired random habitat plots. Habitat metrics at each paired random plot are subtracted from values from the corresponding use plot and serve as values for explanatory variables. Logistic regression is then carried out to fit a response vector of all 1's to a matrix of explanatory variables (Compton et al. 2002). Because probability of use by *H. platirhinos* is low for any given random plot, the use-availability design is approximately equivalent to a case-control design and can be interpreted as such (Keating and Cherry 2004). Odds ratios

approximate the probability that a location will be used given the direction of some variable *x*. More specifically, they describe the proportional change in the probability of use with a one-unit increase in the explanatory variable. Thus, the model is interpreted with respect to differences in habitat between use and random plots, not measured values of habitat parameters. Deviance squared was used to assess fit of the models. Plot data was used as the experimental unit (i.e., each plot was assumed to be independent, see Scope and Limitations). To prevent unequal numbers of plots collected among individuals from biasing results, coefficients were weighted proportionally to the number of relocations for that individual such that each individual supplies equal weight to model parameter estimates. All possible subsets were considered as candidate models. We ranked models using Akaike's Information Criterion scores corrected for small sample sizes (AIC_c), and models with the lowest AIC_c score were considered most supported (Burnham and Anderson 2002).

All movement parameters were calculated using the Hawth's Tools extension for ArcGIS 9.2 (ESRI, Redlands, CA). Statistical tests were performed using JMP version 8.0 and 9.0 (SAS Institute Inc., Cary NC), and R version 2.13.2, (R Development Core Team, Vienna, Austria). All means are reported $\pm$ SE, and tests were considered significant at $\alpha=0.05$.

Results

Radiotelemetry and Data Collection

Sixteen snakes (10 females, 6 males) were radiotracked during the two year duration of the study. Individuals were relocated approximately once every 4 days from the

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beginning of May to the end of August (mean = 4.17 days, SE = 0.13, n = 315

relocations) and approximately once every 12.5 days during September and October

(mean = 12.46 days, SE = 1.08, n = 54 relocations). Snakes were also radiotracked when

possible during late fall and early spring. Duration of radiotracking averaged 191

calendar days per snake (mean = 191.4 days, SE = 47.0, range = 1-553 days, n = 16

individuals), and individuals were relocated on average approximately 26 times (mean =

25.8 days, SE = 4.8, n = 16 individuals) prior to death/signal loss/end of study. A total of

413 relocations were logged over two years. Five snakes were radiotracked during both

years (Table 2.2).   A total of 363 body temperature observations were taken in two years

(Chapter 1).

Movements

  Snake ADMs were right skewed with females exhibiting the longest movements (Figure

2.3). Fourty-one of the 50 longest (82%) ADMs were made by females with Snake D

accounting for 9 of the 10 longest (90%) ADMs. Female ADM was 28.9 m/d (SE = 5.2,

n = 8 individuals) with snake D and 24.6 m/d (SE = 3.2, n = 7 individuals) without snake

D. Male ADM was 18.6 m/d (SE = 2.7, n = 5 individuals). ADM between sexes was not

significantly different (Z = -0.805, P = 0.421). Mean ADMs for all observations (n =

387) are separated by sex and month in Figure 2.5. ADM in females was greatest in July

and smallest in September and October, while male ADM was greatest in September and

smallest in June. Fifteen of the 30 longest (50%) ADMs took place in July. When mean

ADM was calculated for each individual in each month and tested for differences

between sexes, the only month that produced a statistically significant difference was

July (Z = -2.00, P = 0.045). ADMs are reported in Figure 2.6 (along with body

temperature and body mass) for each individual by years in which they were relocated a minimum of 10 times.

Total linear distance moved was calculated for all individuals and was highly correlated with number of relocations ($r^2 = 0.71$, $P = <0.001$, slope = 248.8). This relationship was similar for both sexes (females: $r^2 = 0.71$, $P = 0.009$, slope = 266.5; males: $r^2 = 0.74$, $P = 0.061$, slope = 183.9). Snake D exhibited the greatest distance moved for females (19668.9 m), and Snake I exhibited the greatest distance moved for males (8411.2 m).

Home Range

Mean MCP size was greater for females (mean = 39.6 ha, SE = 24.9, $n = 8$ individuals) than males (mean = 17.1 ha, SE = 8.8, $n = 5$ individuals), however the MCP for snake D greatly inflated the female mean. Female mean MCP size without snake D was 15.3 ha (SE = 6.6, $n = 7$ individuals). Despite the disparity in results dependent upon snake D, the point was not excluded from analysis assessing differences in home range size between sexes because a nonparametric rank sums test was used. There was no significant difference in MCP size (Z = 0.000, $P = 1.00$) or KDE size (Z = 0.000, $P = 1.00$) between sexes. There was a significant positive correlation between the number of relocations and MCP size ($r^2 = 0.49$, $P = 0.007$, slope = 2.26). However, when snake D was removed from this analysis the relationship was not significant ($r^2 = 0.28$, $P = 0.076$, slope = 0.639). There was a similar relationship between the number of relocations and KDE size (with snake D: $r^2 = 0.29$, $P = 0.053$, slope = 1.16; without snake D: $r^2 = 0.01$, $P = 0.757$, slope = 0.149). There was no significant relationship between SVL and MCP size ($r^2 = 0.137$, $P = 0.212$, slope = 0.214), though the relationship between SVL and KDE size was approaching significant ($r^2 = 0.295$, $P = 0.055$, slope = 0.206).

Mean 95% KDE size (mean = 29.3 ha, SE = 10.3, n = 13 individuals) was similar to mean MCP size (mean = 31.0 ha, SE = 15.6, n = 13 individuals), though estimates for individual snakes varied widely with certain KDEs exceeding MCP estimates (e.g., snake O) and others falling below MCP estimates (e.g., snake D). A paired t-test revealed no statistical difference between MCP size and KDE size (t_{12} = -0.236, P = 0.82). Mean core area (50% KDEs) was 5.7 ha (SE = 1.8, n = 13 individuals), and was similar between sexes when snake D was not considered (Z = 0.324, P = 0.745). MCP size and core area size were positively correlated (r^2 = 0.74, $P < 0.001$, slope = 7.35).

Individuals radiotracked in both years demonstrated considerable overlap in annual home range (Table 2.4). Annual MCPs for snake D were strikingly similar in size and orientation; she appeared to use the same area in both years for oviposition and subsequent foraging, though she brumated in different areas (1944 m between hibernacula). Snakes D and I exhibited substantial core use overlap between years (44.3 and 40.8%, repectively). There was no overlap in core use for snake H, but MCP overlap was 79.3% and she exhibited fidelity to the same hibernaculum in consecutive years (Buchanan et al. in *press*). Annual MCPs with all relocations are shown for these individuals in Figure 2.7. Of 12 instances where individuals were radiotracked to hibernacula, 9 of these locations represented perimeter points of annual MCPs, indicating that hibernacula were usually located towards the extent of an individual's annual home range.

Habitat Selection

A total of 126 snake use and 126 paired random habitat plots were collected for 11 individuals, with numbers of plots collected for each snake ranging from 3 to 24.

Logistical constraints prevented more habitat data from being collected. Means for differences between use and random plots for each variable are presented for each snake in Table 2.5. *Leaf.litter* and *grass.sedge* (excluding ammophila) were the variables with the greatest positive mean difference between use and random plots at the 1 m^2 scale (suggesting snake preference). *Open.soil* and *cranberry* were the variables with the greatest negative mean difference between use and random plots at the 1 m^2 scale (suggesting snake avoidance; but see Discussion). Results were similar at the 15 m radius scale with *grass.sedge* (including ammophila) and *leaf.litter* exhibiting the greatest positive mean difference and *open.soil* and *cranberry* exhibiting the greatest negative mean difference.

Grass.sedge was the top AIC$_c$ ranked model at both scales (Table 2.6) with a deviance squared value of 0.319 at the 1 m^2 scale and 0.178 at the 15 m radius scale. All models within two AIC units of the top models are presented in Table 2.6. Model weights were considerably deflated due to the large number of models assessed in the analysis. Coefficients and odds ratios are provided for all variables in the top three models at both spatial scales in Table 2.7.

Discussion

Spatial Ecology

The concept of home range dates at least from Burt (1943) when it was defined as the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range." While this definition is

conceptually adequate, it is vague and limited in usefulness when attempting to quantify

the extent of an animal's spatial use with radiotelemetry data. White and Garrot (1990)

support a more precise definition using a probability level of 95% of the locations an

animal occurs in throughout its lifetime. While this is helpful in standardizing estimates

of home range between studies, it is arbitrary and may not factor in important differences

in resource distribution between study sites or different evolutionary strategies between

species. Nonetheless, the delineation of home range remains a fundamental effort of

biologists studying spatial use in wildlife (Alfred et al. 2012, Kapfer et al. 2010,

Rasmussen and Litzgus 2010), and with good reason as these estimates serve as

important input for ecological analyses.

  Because minimum convex polygons (MCPs) are the technique least subject to

misinterpretation given different quantities of data between individuals and have been

recognized as the preferred method in studies of snakes (Gregory et al. 1987), they are

generally considered the best home range estimates for comparison with other studies.

Kernel density estimates (KDEs) were also reported for continuity with other studies of

H. platirhinos (Lagory et al. 2009), though divergences in smoothing factors between

studies makes comparison difficult (Downs and Horner 2008, Hemson et al. 2005).

Confounding comparisons further is the duration of time which to consider when

calculating a home range. Certain studies make home range estimates annually

(Plummer and Mills 2000), others pool data for multiple years, when possible (Moore

and Gillingham 2006). Both annual and pooled MCPs are reported in this study (Tables

2.3 and 2.4), though only MCPs consisting of all available data were considered for

statistical analysis.

Average daily movements (ADMs) did not vary significantly between sexes when pooled over the course of the activity season, but when separated by month differences were apparent. Female movements were greatest in July and least in September and October. In the case of gravid females, movements appeared to peak immediately after oviposition (Figure 2.6). This was likely a response to an increase in foraging once eggs were deposited and/or a movement away from locations selected based on their suitability as nest sites (Burger and Zappalorti 1986, Scott 1985). Male movements were greatest in July, September and October. Increased movements in September and October were perhaps a reflection of mate searching (Cunnington and Cebek 2005, Gregory et al. 1987, Platt 1969, Plummer and Mills 1996). Plummer and Mills (2000) observed similar seasonal differences in movements in males and females. This despite a much higher estimate of daily movement of 119 m (SD = 4, n = 8 individuals) in their study.

There was no difference in home range size between sexes in our study, though individual home range estimates varied widely. Home range measurements for snake D represent what are probably extremes in *H. platirhinos,* especially among females. Plummer and Mills (2000) report a maximum *H. platirhinos* annual MCP of 72.8 ha (a male) and a mean annual MCP of 50.2 ha (SD = 6.4, n = 8 estimates) from their study site in Arkansas. It should be noted however, that they subjectively removed "temporary sojourns which seemed not to be normal day-to-day home range movements" from their estimates. Lagory et al. (2009) report a maximum *H. platirhinos* pooled MCP of 91.6 ha (a male) and a mean pooled MCP of 51.7 ha (SE = 14.7, n = 8 individuals) at their study site in New Hampshire. They report a mean core size (50% KDE) of 6.5 ha (SE = 1.4, n = 8 individuals). The mean home ranges reported in these two studies represent

relatively large estimates for snakes (Macartney et al. 1988). Large home range size of

H. platirhinos may make the species more prone to fragmentation by roads and

development and may have implications for the amount of land conserved for protection

of vulnerable populations (Gibbons et al. 2000). Roads serve as a barrier to many

wildlife species both directly, via mortality, and indirectly, via avoidance (Forman and

Alexander 1998). Interestingly, no snakes crossed paved roads during the course of our

study. Snake D was found within 5 m of a paved road at the eastern extent of her home

range in 2009, but soon after reversed course and returned to the adjacent pine forest.

Certain home ranges appeared to have an orientation running parallel to nearby paved

roads, though the effect of the road is unclear (Figure 2.4). Andrews and Gibbons (2005)

report a high rate of road avoidance in *H. platirhinos* relative to 8 other species studied.

It is clear however, that *H. platirhinos* do move onto roads in our study site as evidenced

by road mortality data collected by the National Park Service. Between 2001-2011, 10

H. platirhinos were found dead on roads within CCNS (R. Cook, US National Park

Service, Wellfleet, MA, 2010 unpubl. data). The degree to which roads influence

landscape permeability in snakes and other wildlife at CCNS is a question with

significant conservation implications, especially with respect to U.S. Highway 6 which

bisects the narrow peninsula in a (mostly) north-south direction.

  Home range estimates and daily estimates of movement were smaller in our study than

in other studies of *H. platirhinos* (Lagory et al. 2009, Plummer and Mills 2000). This

may suggest a greater availability of resources (i.e., density of prey, availability of mates)

and critical habitat (i.e., nest sites, hibernacula) at our study site (Carfagno and

Weatherhead 2008, Kapfer et al. 2010, Plummer and Congdon 1994). The Province

Lands area of CCNS is interspersed with an abundance of temporary wetlands which serve as seasonal breeding sites for toads. A high density of these prey items at our study site, as has been noted in the field, would likely reduce the movements of snakes. Hibernacula were usually located (9/12, 75%) at the outer edge of home ranges which may be a result of migratory movements in search of appropriate hibernacula sites. Alternatively, this could simply be a reflection of late-season movements (perhaps in association with mate searching) and an associated expanse in home range size. If hibernacula sites were not limiting in our study area we would expect snakes to brumate in the vicinity of their late season location. Individuals radiotracked in consecutive years exhibited fidelity to certain areas, and in certain cases movements represented use of a single, well-defined area (Figure 2.7). Plummer and Mills (2000) observed similar patterns in *H. platirhinos* in Arkansas and other studies have observed similar patterns in different species of snakes (Diffendorfer et al. 2005). Observations from this study raise important questions regarding inter-annual fidelity to specific sites especially as they pertain to critical habitat features such as nest sites and hibernacula. These questions should be addressed in future studies, especially in areas where critical habitat features are suspected to be limiting as these sites play a disproportionate role in ensuring prolonged viability of populations (Shine 2003, Shine and Bonnett 2009).

Snake D exhibited extraordinary use of space in both years that she was radiotracked. The movement parameters of this individual far exceeded those of any other snake (Tables 2.2 and 2.3). The obvious difference between snake D and other individuals was geographic location; snake D was the only individual located at the eastern extent of the study area where the post-glacial, early successional Province Lands merge with the

pitch-pine dominated forests of the glacial outwash plain of the Outer Cape. Differences in resource availability and habitat characteristics between these two regions of the study area could have influenced movements. Other radiotelemetry studies have documented "transient" behavior in reptiles (Kiester et al. 1982, Lovich 1990), but strong annual home range overlap in snake D preclude this as an explanation for increased movements. It is not uncommon for radiotelemetry data to yield pronounced variation in movements within a population and thus questions remain regarding within-population variation in spatial use.

Habitat Selection

Habitat selection in animals is usually considered at multiple scales. Johnson (1980) introduced the concept of selection order in which increasing orders of habitat selection represent successively finer spatial scales. The habitat selection schemes designed and implemented in this study were intended to assess third (15 m radius) and fourth order (1 m^2) selection which are described as the usage of various habitat components within the home range (third order), and the selection of features from those available at the site that lead to procurement of resources (fourth order) (Johnson 1980). The habitat modeling scheme employed was intended to examine the use of particular habitat components relative to their availability as selectable habitat. If resources were used disproportionately to their availability, selection was inferred (Alldredge et al. 1998).

H. platirhinos exhibited differential selection of certain habitat features at our study site. Deviance squared values at the 1 m^2 level were greater than those at the 15 m radius level suggesting greater selection at the finer spatial scale. Grass and sedge (*grass.sedge*) cover was the variable that had the greatest influence on snake use at both scales.

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Deschampsia flexuousa is a common grass at our study site that occurs both in grassland dunes and among shrubs and stunted pine trees. Snakes were noted to use these cover types with regularity. This selectivity may indicate grasses as an important vegetative feature utilized by *H. platirhinos* for cover; on several occasions individuals were found coiled at the base of a clump of *D. flexuousa*. Alternatively, as grasses and sedges were wide spread in most cover types that supported any vegetation at all, this variable may have had a strong relationship with snake use because snakes tended to avoid areas with no vegetation (i.e., *open.soil*). Leaf litter was another important cover class explaining snake use and was most abundant underneath pine trees and deciduous shrubs and least abundant in areas of open sand. Individuals were regularly found atop and underneath sprawling mats of fallen pine needles; an indicator of leaf litter serving as an important means of refuge and cover from predators. Cunnington et al. (2008) demonstrated that leaf litter is associated with relatively cool ground surface temperatures; it is likely that leaf litter also serves as important thermoregulatory habitat for *H. platirhinos*. Open soil and cranberry were two variables in which the available coverage exceeded that used by snakes. Avoidance by snakes of open soil is not difficult to understand, as time spent in these areas greatly increases the risk of predation. To interpret the results as "avoidance" of cranberry wetlands though, would probably be spurious. On multiple occasions individuals were observed to spend extended periods of time in or near cranberry wetlands, presumably to increase the likelihood of foraging success. It may be expected that *H. platirhinos* association with these temporary wetlands would be correlated with the several week long peak breeding period of their primary source of prey at our study site, *Anaxyrus fowleri* (Cook et al. 2011). If sampling is not carried out throughout the

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entire activity season, such events can easily go undetected. Moreover, if snakes move closer to, but not into wetlands in order to forage for toads, this would increase the probability of recording cranberry as "available" habitat, thus increasing the chances of availability outweighing use in habitat analysis.

Scope and Limitations

All interpretation of results as reflective of the population at large assumes that the snakes located in this study represent a random sample. Because of the manner in which snakes were collected, there is no way of ensuring that this is the case. This is usually an unavoidable scenario with radiotelemetry studies, especially those dealing with species that are difficult to detect (White and Garrott 1990). Most often research proceeds without confronting this dilemma in any direct way.

Differences in the duration and seasonality of radiotracking can make comparisons of movements and home range between snakes difficult. Because snake movements increase during certain times of the year, ideally one should not only collect an adequate number of relocations but should collect data throughout the entire activity season in order to accurately estimate home range. One could take this to its logical end and argue that any calculation of home range made without monitoring an individual over the course of its entire life represents an underestimate. Unfortunately, such an effort was well beyond the logistical constraints of this study (and the vast majority of studies). Differences in the frequency of relocation and/or the duration of radiotracking can alter sampling bias when estimating movements. These factors make comparison of movements and home range difficult between studies, and effort should be made by

researchers to mimic as closely as possible the methodology of previous studies of the

same species (or similar species) if comparison of spatial parameters is a priority.

 Thomas and Taylor (2006) recommend using animals, rather than their relocations, as

the experimental unit when conducting use-availability habitat studies. It is unreasonable

to assume that habitat plots from the same individual are independent as strong

preference by an individual for certain features could bias results. Despite this,

relocations were considered as the experimental unit due to a small number of animals

used in habitat analysis ($n = 11$). To prevent unequal numbers of plots collected among

individuals from biasing results, data were weighted proportionally to the number of

relocations such that each individual's contribution to the estimate of coefficient is equal.

This prevents individuals with a greater number of relocations from disproportionately

influencing model parameter estimates, but due to wide variation in the number of plots

collected per individual, this is still a less than perfect approach to pooling data. Future

research efforts should strive to collect an equal number of habitat plots for each

individual and obtain as many individuals as possible. Furthermore, shifts in resource

use over the course of the year can easily be missed if sampling is not adequately

distributed throughout the activity season (Alldredge et al. 1998, Thomas and Taylor

2006).

Conclusions

 Enhanced understanding of spatial ecology and habitat selection will help focus

conservation and management efforts for *H. platirhinos*. We observed a large variation

in home range size among individuals and seasonal differences in movements between

sexes. Female movements peaked in July, apparently in response to oviposition and an

increased need to forage and/or move away from habitat selected for nesting. Male

movements peaked in September and were probably associated with mate searching.

Estimates of daily movements were less than estimates derived from other studies on *H.*

platirhinos, perhaps indicating a relative abundance of resources at our study site.

Differences in our study compared to other studies of *H. platirhinos* highlight the

importance of multiple radiotelemetry studies in different geographic locales in order to

obtain a more comprehensive range-wide ecological understanding for a given species.

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Table 2.1a. Variables for 1 m^2 habitat analyses for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Variable	Description
ammophila	% cover of *Ammophila sp*. within 1 m^2 quadrat
cranberry	% cover of cranberry within 1 m^2 quadrat
cwd	% cover of course woody debris within 1 m^2 quadrat
decid.shrub	% cover of deciduous shrubs within 1 m^2 quadrat[a]
dwarf.shrub	% cover of persistent dwarf shrubs within 1 m^2 quadrat
grass.sedge	% cover of grass/sedge (except ammophila) within 1 m^2 quadrat
herb	% cover of perennial herbaceous plants within 1 m^2 quadrat
leaf.litter	% cover of leaf litter within 1 m^2 quadrat
lichen	% cover of lichen within 1 m^2 quadrat
moss	% cover of moss within 1 m^2 quadrat
open.soil	% cover of open soil within 1 m^2 quadrat
pinus	% cover of *Pinus* sp. within 1 m^2 quadrat
poison.ivy	% cover of poison ivy within 1 m^2 quadrat
densiometer	percent of canopy coverage as measured from center of 1 m^2 quadrat
dist.to.edge	distance to nearest edge (m)
mean.litter.depth	mean of four leaf litter depth measurements from within 1 m^2 quadrat (cm)

[a] highest percentage retained as measured separately for the following*: Quercus ilicifolia, Rosa rugosa, Myrica pensylvanica, Kalmia latifolia, Vaccinium angustifolium*

Table 2.1b. Variables for 15 meter radius habitat analysis for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Variable	Description
cranberry	mean % cover of cranberry
creeping.pine	mean % cover of *Pinus* sp. below 1m height
elevated.pine	mean % cover of *Pinus* sp. above 1m height
cwd	mean % cover of course woody debris (>2cm diameter)
dec.shrub	mean % cover of deciduous shrubs
dwarf.shrub	mean % cover of dwarf shrub
grass.sedge	mean % cover of graminoids (including *Ammophila* sp.)
herb	mean % cover of perennial herbaceous plants
leaf.litter	mean % cover of leaf litter
moss.lichen	mean % cover of moss or lichen
open.soil	mean % cover of open soil
sdw	mean % cover of standing dead wood
densiometer	mean % canopy coverage as measured from center of each quadrat
mean.litter.depth	mean depth of leaf litter as measured from 4 points in each quadrat

Table 2.2. Summary of data collection and movements for *H. platirhinos* at Cape Cod National Seashore 2009-2010[a]

Snake	Sex	Dates radiotracked	Duration of dates tracked	Number of relocations	Total linear distance moved (m)	Mean distance between relocations (m)	Avg. daily movements(m/d) (May-August only)	Number of habitat plots established
A	M	051109-051909	8	3	-	-	-	-
B	F	051209-070109	50	18	875.3	51.5	24.3	10
C	F	051609-053109	15	7	-	-	-	4
D	F	051609-112010	553	66	19668.9	322.4	59.5	24
E	F	052209-052309	1	1	-	-	-	-
F	F	053009-071109	42	14	615.3	47.3	14.2	10
G	M	061309-052510	346	34	2249.6	75.0	13.8	11
H	F	061309-101710	491	59	5905.7	105.5	25.4	22
I	M	072709-101710	447	48	8411.2	191.2	27.8	16
J	F	081209-091710	401	41	4570.1	123.5	24.4	11
K	F	060410-101710	135	24	3708.0	161.2	41.1	3
L	F	060410-101610	134	26	2940.3	117.6	24.7	8
M	M	060410-082610	83	20	1769.4	93.1	24	7
N	F	061810-102210	126	20	1381.3	72.7	18	-
O	M	062610-101710	113	14	2274.7	175.0	28.8	-
P	M	062610-102210	118	18	941.7	55.4	11.5	-
Female Mean (*n* = 8)	-	-	194.8	33.5[b]	4958.1	125.2	28.9	-
(SE)	-	-	(65.4)	(6.9)	(1342.3)	(31.3)	(5.2)	-
Male Mean (*n* = 5)	-	-	185.8	26.8[b]	3129.3	117.9	18.6	-
(SE)	-	-	(69.8)	(6.3)	(1342.3)	(27.4)	(2.7)	-
Total Mean (*n* = 13)	-	-	191.4	30.9[b]	4254.7	122.4	25.9	-
(SE)	-	-	(47)	(4.8)	(1427.1)	(21.2)	(3.5)	-

[a]Minimum 14 relocations required for movement parameters
[b]Includes only individuals for which movement parameters were calculated

Table 2.3. Home range estimates for *H. platirhinos* at Cape Cod National Seashore 2009-2010[a].

Snake	Sex	Dates radiotracked	Number of relocations	MCP (ha)	95% KDE (ha)	50% KDE (ha)
B	F	051209-070109	18	1.9	3.4	0.7
D	F	051609-112010	66	209.3	131.3	21.5
F	F	053009-071109	14	1.0	2.8	0.5
G	M	061309-052510	34	8.4	8.4	2.0
H	F	061309-101710	59	22.4	16.0	3.0
I	M	072709-101710	48	51.1	35.0	7.1
J	F	081209-091710	41	21.8	24.7	5.5
K	F	060410-101710	24	49.0	73.1	16.6
L	F	060410-101610	26	8.0	19.7	3.1
M	M	060410-082610	20	9.7	10.5	2.5
N	F	061810-102210	20	3.3	4.2	1.0
O	M	062610-101710	14	15.1	47.4	9.0
P	M	062610-102210	18	1.4	3.7	0.9
Female Mean (*n* = 8)	-	-	-	39.6	34.4	6.5
(SE)	-	-	-	24.9	16	2.8
Male Mean (*n* = 5)	-	-	-	17.1	21	4.3
(SE)	-	-	-	8.8	8.5	1.6
Total Mean (*n* = 13)	-	-	-	31.0	29.3	5.7
(SE)	-	-	-	15.6	10.3	1.8

[a] Home range estimates were calculated using all relocations

Table 2.4. Annual home range estimates for *H. platirhinos* radiotracked at Cape Cod National Seashore 2009-2010[a]

Snake	Sex	2009 MCP	2009 core area	Number of 2009 relocations	2010 MCP	2010 core area	Number of 2010 relocations	% overlap of MCPs[b]	% overlap of core areas (50% KDEs)[c]
D	F	133.9	13.2	38	171.9	26.7	28	81.3	44.3
G	M	7.0	1.6	28	-	-	6	-	-
H	F	7.3	1.4	27	17.8	3.4	32	79.3	0
I	M	17.1	9.1	15	35.3	9.3	33	81.6	40.8
J	F	-	-	11	14.3	4.2	30	-	-

[a]Minimum 14 relocations required for calculation of home range
[b]Calculated as area of overlapping 2010 MCP/2009 MCP
[c]Calculated as area of overlapping 2010 KDE/2009 KDE

Table 2.5a. Differences between 1 meter square use and paired random means for all variables by snake for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Snake	ammophila	cranberry	cwd	decid.shrub	dwarf.shrub	grass.sedge	herb	leaf.litter	lichen	moss	open.soil	pinus	poison.ivy	densiometer	dist.to.edge	mean.litter.depth
B	0.0	-7.8	0.5	-2.0	-0.6	20.4	2.1	26.2	-14.4	-8.8	-14.8	33.3	0.0	4.4	0.3	2.5
C	-17.5	-48.8	0.0	-2.5	0.0	47.3	-0.5	14.3	2.5	0.5	3.8	0.0	27.5	-7.0	2.4	-0.5
D	-0.2	-6.3	-2.2	29.2	0.8	32.2	-0.1	21.7	-0.1	-1.7	-9.8	-9.2	15.8	-12.5	-4.5	0.1
F	-1.1	0.0	-0.4	17.5	0.0	45.5	-8.6	19.6	2.1	-0.4	-37.4	0.0	-4.0	0.0	-10.2	0.4
G	3.3	22.2	-4.1	6.8	-0.1	-7.2	-4.6	12.4	-0.3	-0.7	-11.4	1.2	0.0	7.0	-0.2	1.0
H	12.4	3.3	5.8	10.8	-2.9	9.5	-0.2	46.7	-7.0	-0.9	-44.2	21.0	0.8	15.1	-2.9	3.1
I	-1.5	0.0	-2.0	39.0	-0.7	40.4	-0.6	49.2	1.6	0.0	-45.3	0.0	10.7	-0.4	-2.1	1.7
J	3.7	0.0	0.2	29.5	0.0	28.7	0.5	34.9	-0.7	-0.9	-35.0	2.2	-2.3	-9.5	-1.3	0.9
K	15.0	0.0	6.3	44.3	0.0	33.0	0.0	82.3	-4.7	0.0	-79.7	-6.7	-0.3	16.8	0.5	3.1
L	0.0	-23.8	-3.1	-8.8	-11.9	2.0	-0.3	13.9	-2.9	-1.3	-3.8	76.0	0.0	-32.0	-0.3	3.0
M	0.0	-13.9	0.1	8.4	-6.6	19.0	4.0	12.9	-0.1	0.0	-11.3	22.4	-1.3	3.5	-2.2	0.5
% Positive	36.4	18.2	45.5	72.7	18.2	90.9	27.3	100.0	27.3	9.1	9.1	54.5	36.4	45.5	27.3	90.9
Mean	1.3	-6.8	0.1	15.7	-2.0	24.6	-0.7	30.4	-2.2	-1.3	-26.3	12.7	4.3	-1.3	-1.9	1.4
SE	2.5	5.4	1.0	5.3	1.2	5.3	1.0	6.5	1.5	0.8	7.4	7.5	2.9	4.1	1.0	0.4

Table 2.5b. Differences between 15 meter radius use and paired random means for all variables by snake for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Snake	cranberry	creeping.pine	elevated.pine	cwd	dec.shrub	dwarf.shrub	grass.sedge	herb	leaf.litter	moss.lichen	open.soil	sdw	mean.litter.depth	densiometer
B	-5.2	1.2	-3.5	-0.3	-9.0	0.8	1.6	-0.5	-14.5	10.8	1.6	-0.7	-0.7	-9.7
C	-30.0	-1.1	-0.2	-1.0	-3.9	0.7	26.1	0.4	-6.8	-0.9	13.6	-0.6	0.0	-10.9
D	-10.2	1.6	2.3	0.5	3.2	-0.4	15.8	6.7	16.5	-0.5	-4.0	1.0	0.2	2.5
F	0.0	0.0	0.0	-0.3	4.3	0.0	7.1	-2.6	2.1	1.1	-3.4	0.0	0.1	0.0
G	-2.2	0.0	11.4	-0.6	-5.4	0.2	-2.5	-2.9	6.7	1.5	5.1	0.2	0.4	9.1
H	0.3	8.1	3.8	0.3	1.4	-1.8	14.2	1.2	19.2	-0.6	-18.1	0.8	0.4	5.3
I	0.0	0.0	0.0	-2.1	12.8	4.4	17.4	9.6	16.5	9.7	-27.6	0.1	0.7	0.0
J	0.0	1.3	4.3	0.9	7.5	-1.1	11.7	2.3	12.1	-5.5	-12.0	1.5	0.5	3.5
K	0.0	-3.8	-0.5	1.3	0.1	-0.1	16.9	1.1	45.0	-4.3	-30.4	0.4	1.8	17.4
L	-19.8	12.5	3.0	-1.9	-8.0	-2.9	5.8	1.3	-14.3	7.1	5.6	-0.3	-0.1	-15.7
M	6.6	3.3	13.0	-0.1	-7.4	-3.0	8.9	-0.3	11.9	-0.2	-9.9	0.2	0.4	-6.8
% Positive	18.2	54.5	54.5	36.4	54.5	36.4	90.9	63.6	72.7	45.5	36.4	63.6	72.7	45.5
Mean	-5.5	2.1	3.0	-0.3	-0.4	-0.3	11.2	1.5	8.6	1.7	-7.2	0.2	0.3	-0.5
SE	3.2	1.4	1.5	0.3	2.1	0.6	2.4	1.1	5.2	1.6	4.2	0.2	0.2	2.9

Table 2.6a. All paired logistic regression modeling results within 2 AIC_c units of top model for 1 m^2 habitat analysis for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Rank	Model	k	Deviance squared	AIC_c	ΔAIC_c	ω
1	*grass*	1	0.319	4.807	0	0.023
2	*leaf.litter + grass*	2	0.452	5.441	0.634	0.017
3	*open.soil + grass*	2	0.474	5.578	0.771	0.016
4	*mean.litter.depth + grass*	2	0.414	6.267	1.46	0.011
5	*ammophila + grass*	2	0.372	6.39	1.583	0.01
6	*poison.ivy + grass*	2	0.334	6.477	1.67	0.01
7	*decid.shrub + grass*	2	0.374	6.787	1.98	0.009
8	*grass + herb*	2	0.323	6.806	1.999	0.009

Table 2.6b. All paired logistic regression modeling results within 2 AIC_c units of top model for 15 meter radius habitat analysis for *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Rank	Model	k	Deviance squared	AIC_c	ΔAIC_c	ω
1	*grass.sedge*	1	0.178	9.51	0	0.031
2	*cranberry*	1	0.045	9.936	0.426	0.025
3	*mean.litter.depth*	1	0.051	10.02	0.51	0.024
4	*cranberry + mean.litter.depth*	2	0.1	10.298	0.788	0.021
5	*cranberry + leaf.litter*	2	0.124	10.476	0.966	0.019
6	*leaf.litter*	1	0.055	10.557	1.047	0.018
7	*cranberry + open.soil*	2	0.135	10.779	1.269	0.016
8	*grass.sedge + mean.litter.depth*	2	0.189	11.145	1.635	0.014
9	*grass.sedge + leaf.litter*	2	0.182	11.406	1.896	0.012
10	*grass.sedge + open.soil*	2	0.189	11.436	1.926	0.012
11	*grass.sedge + cranberry*	2	0.18	11.489	1.979	0.011
12	*open.soil*	1	0.056	11.49	1.98	0.011

Table 2.7a. Top three 1 m^2 paired logistic regression models that explain habitat selection in *H. platirhinos* at Cape Cod National Seashore 2009-2010.

		grass.sedge			leaf.litter			open.soil		
Rank	Model	Coefficient	Odds ratio	Conf. Interval	Coefficient	Odds ratio	Conf.Interval	Coefficient	Odds ratio	Conf. Interval
1	*grass.sedge*	0.0422	1.0431	(1.025, 1.061)	-	-	-	-	-	-
2	*leaf.litter + grass.sedge*	0.0376	1.0383	(1.019, 1.053)	0.0245	1.0248	(1.012, 1.037)	-	-	-
3	*open.soil + grass.sedge*	0.0347	1.0353	(1.018, 1.053)	-	-	-	-0.0443	0.9566	(0.930, 0.984)

Table 2.7b. Top three 15 meter radius paired logistic regression models that explain habitat selection in *H. platirhinos* at Cape Cod National Seashore 2009-2010.

Rank	Model	Coefficient	Odds ratio	Conf. interval
1	*grass.sedge*	0.0560	1.0575	(1.031, 1.085)
2	*cranberry*	-0.0273	0.9731	(0.948, 0.999)
3	*mean.litter.depth*	0.3526	1.4227	(1.052, 1.925)
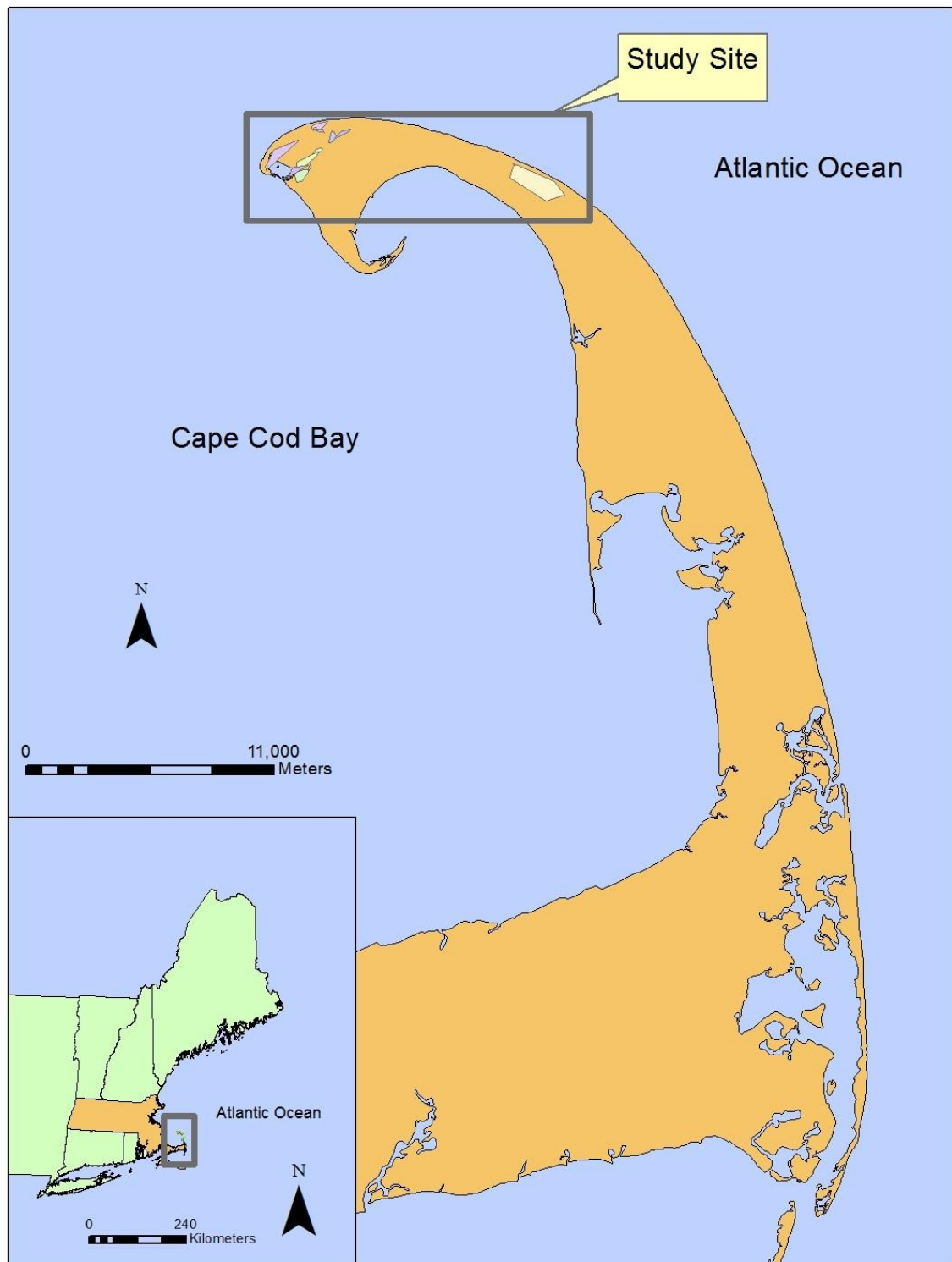
Figure 2.1. Map showing location of study site in Barnstable County, Massachusetts.
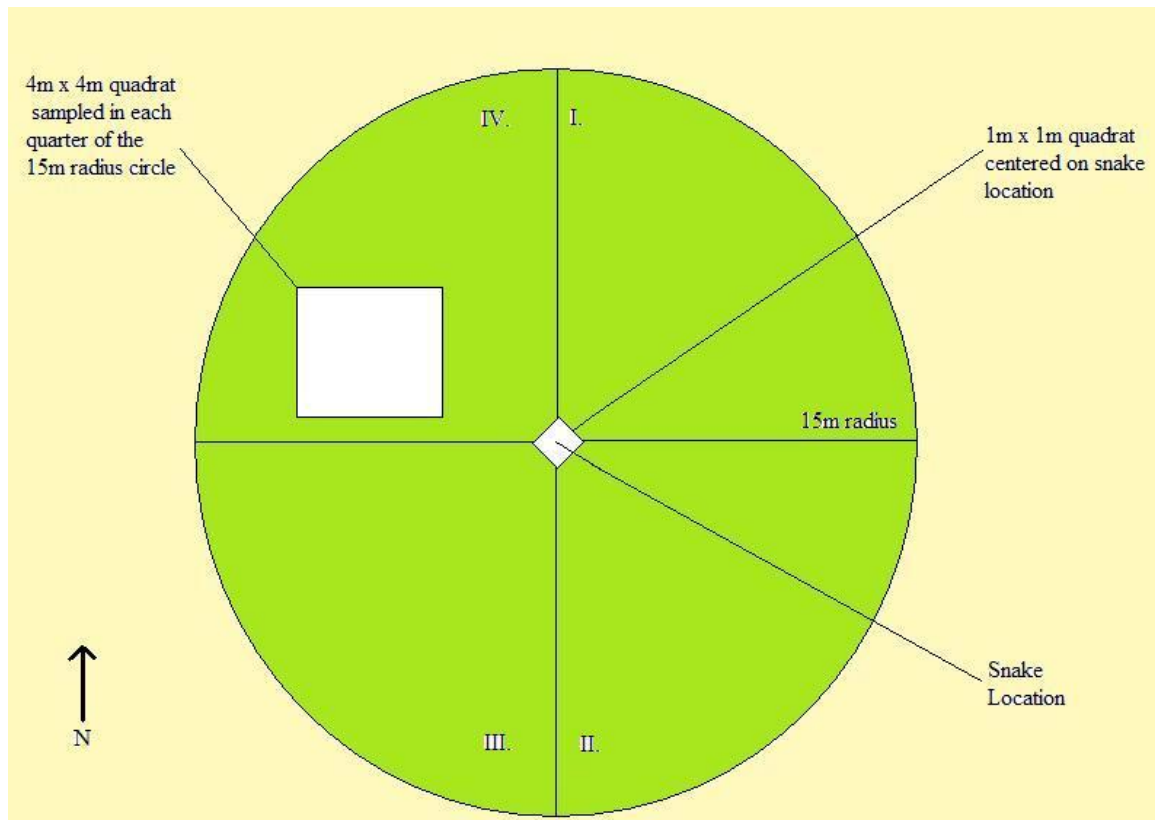
Figure 2.2. Diagram showing the sampling scheme for *H. platirhinos* habitat data collection at the 1 m^2 and 15 m radius spatial scales at Cape Cod National Seashore 2009-2010. Diagram not to scale.
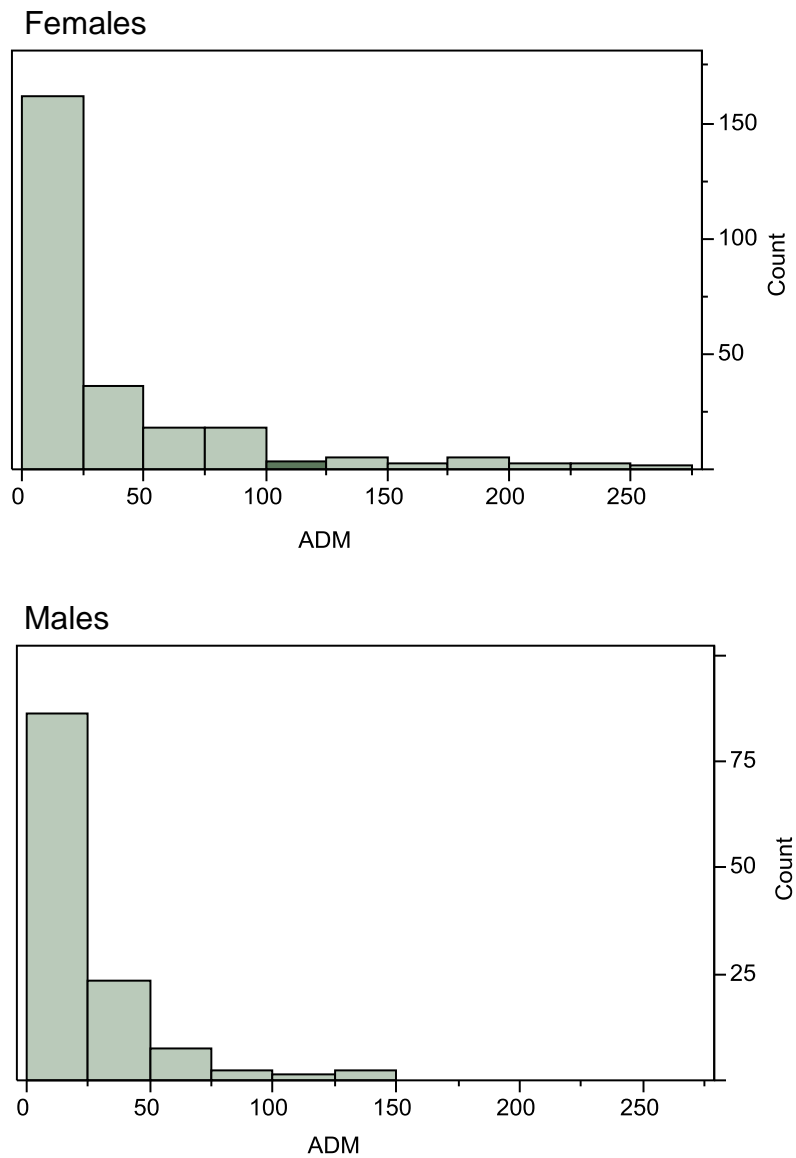
Figure 2.3. Distribution of average daily movements (ADMs) for all observations May-October for male and female *H. platirhinos* at Cape Cod National Seashore 2009-2010.
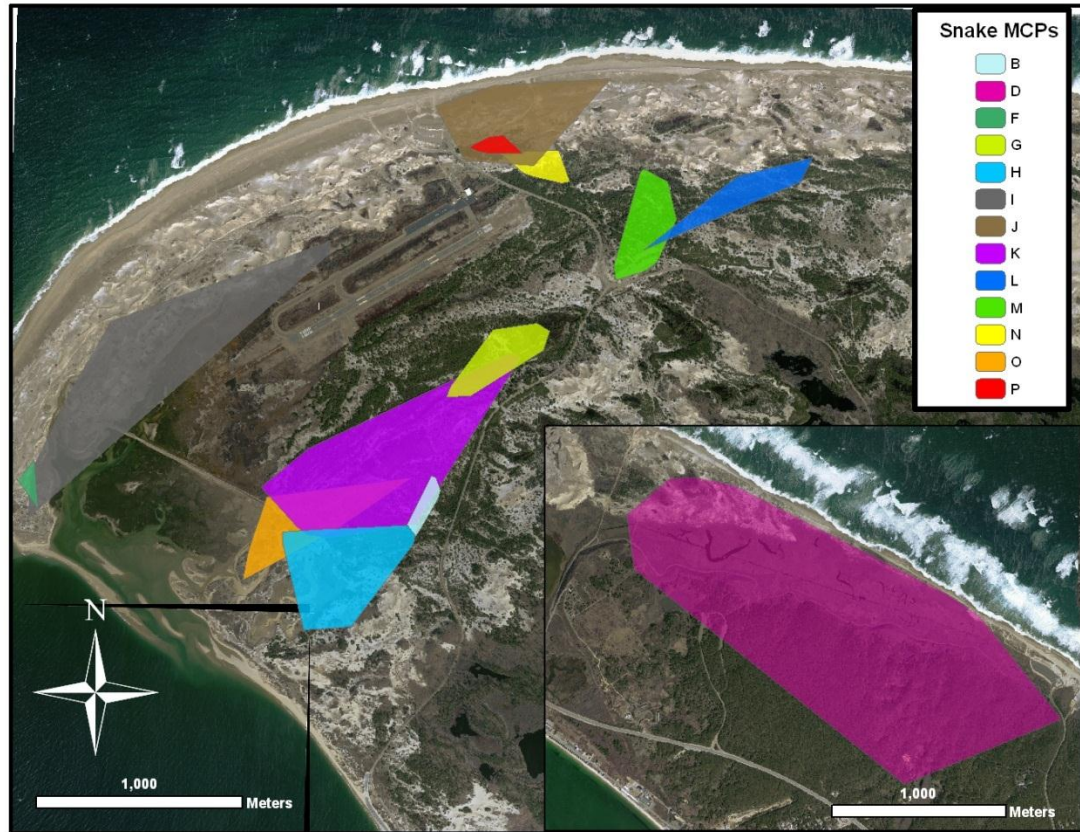
Figure 2.4. Minimum convex polygons (MCPs) of all *H. platirhinos* with ≥ 14 relocations at Cape Cod National Seashore 2009-2010. The inset is snake D located approximately 9 km east of the study area shown containing the majority of the individuals.
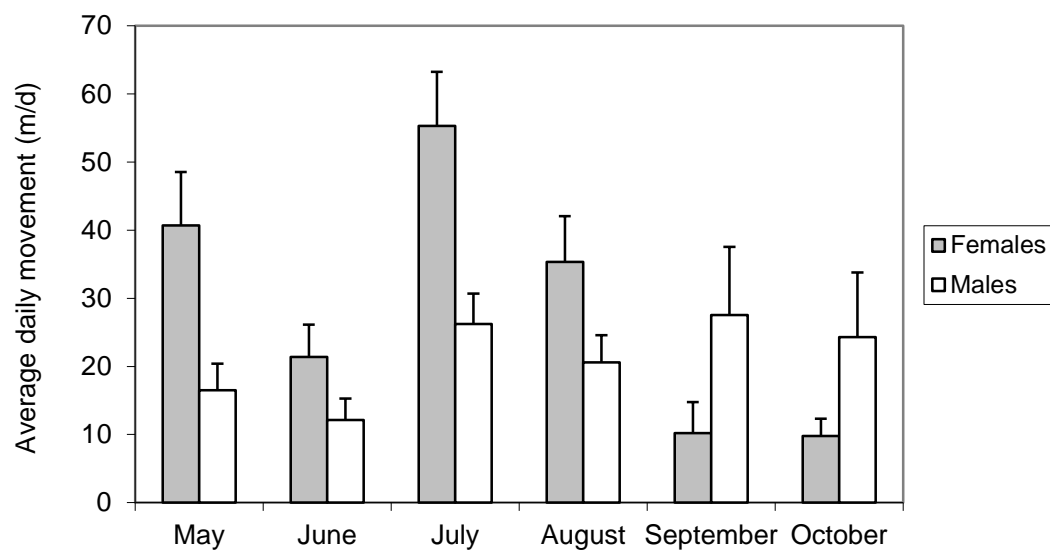
Figure 2.5. Average daily movements (ADMs) by month for all observations of *H. platirhinos* at Cape Cod National Seashore 2009-2010. Error bars are standard errors.

Figure 2.6a. Gravid females.

Snake H

Snake H

95

Snake K

Snake L

Dat
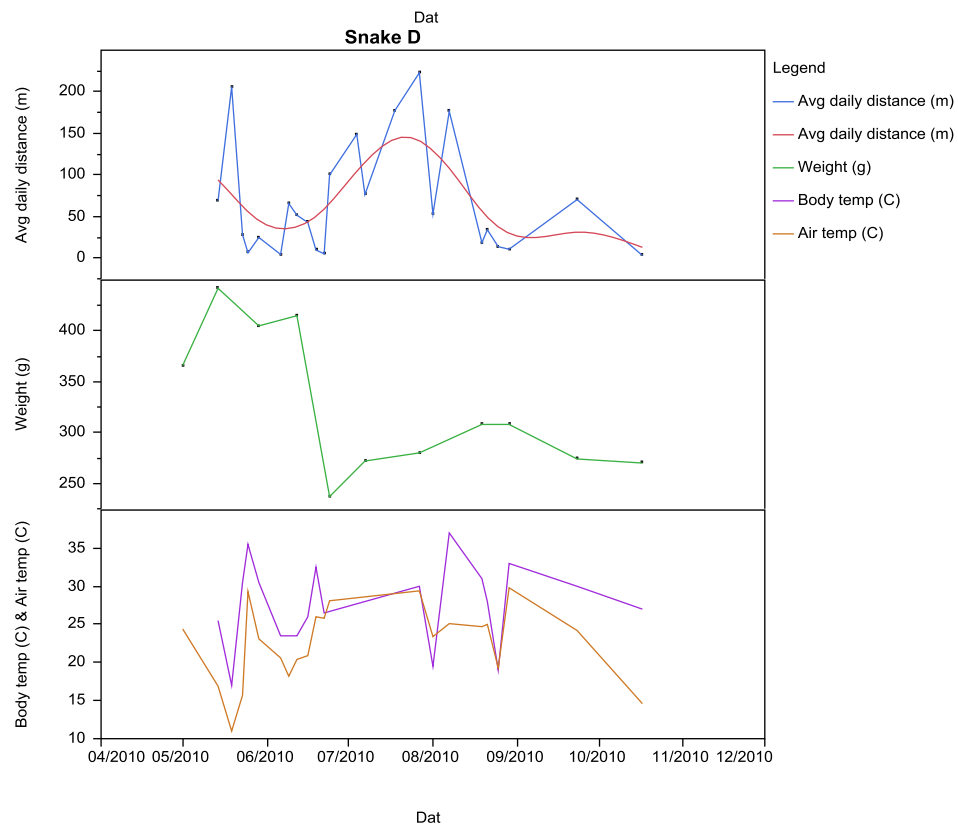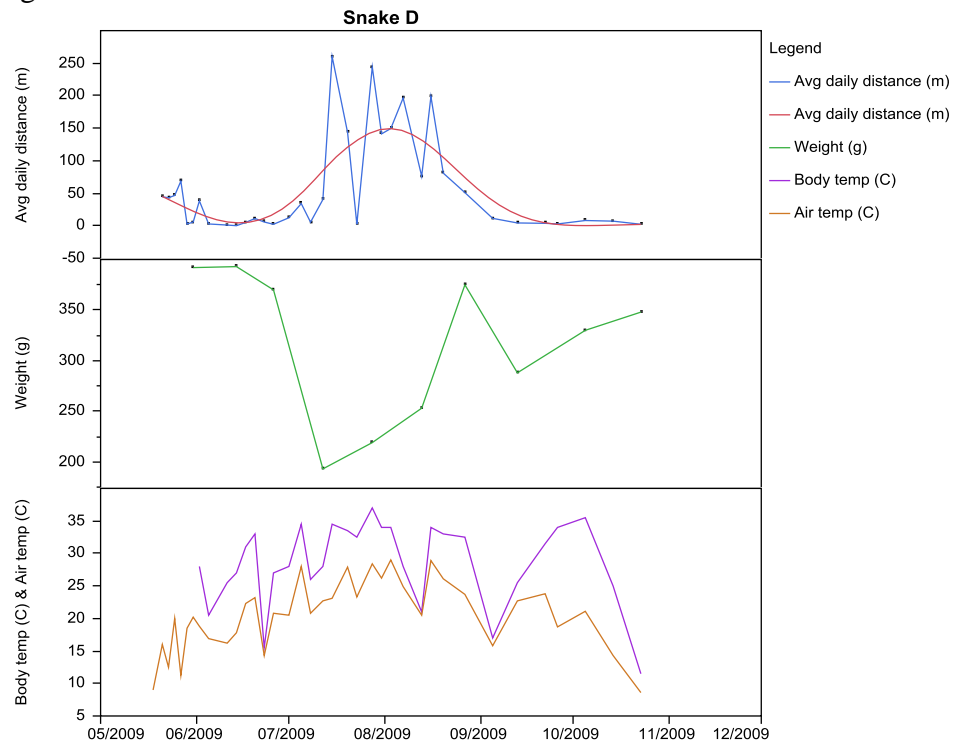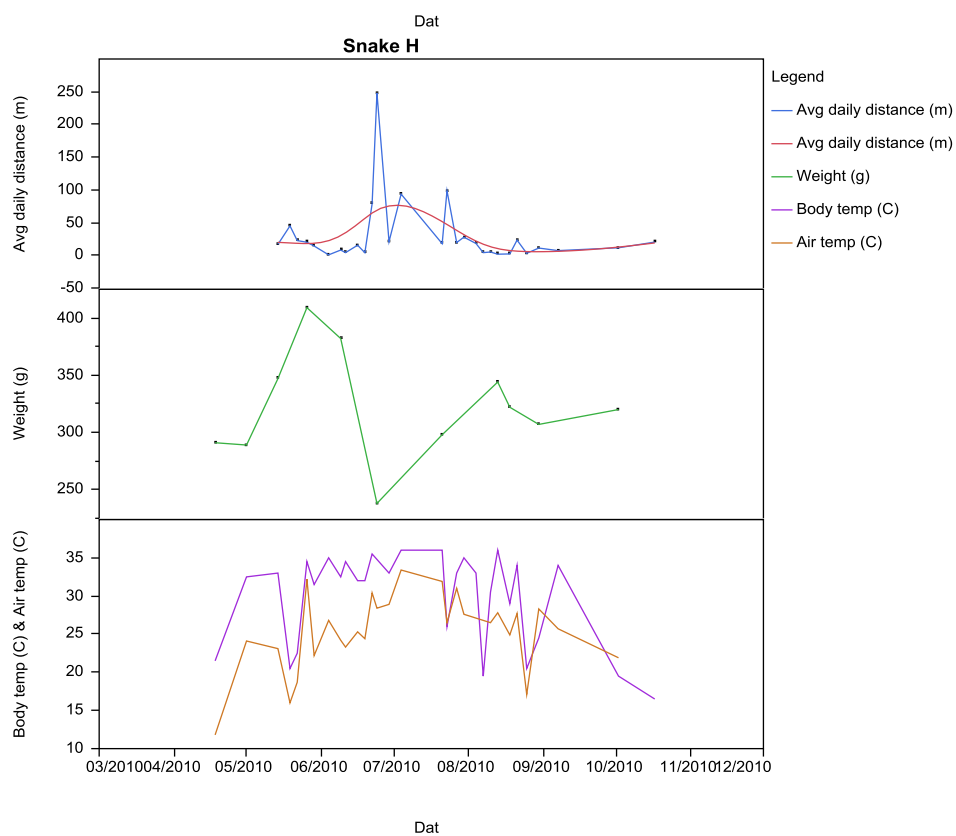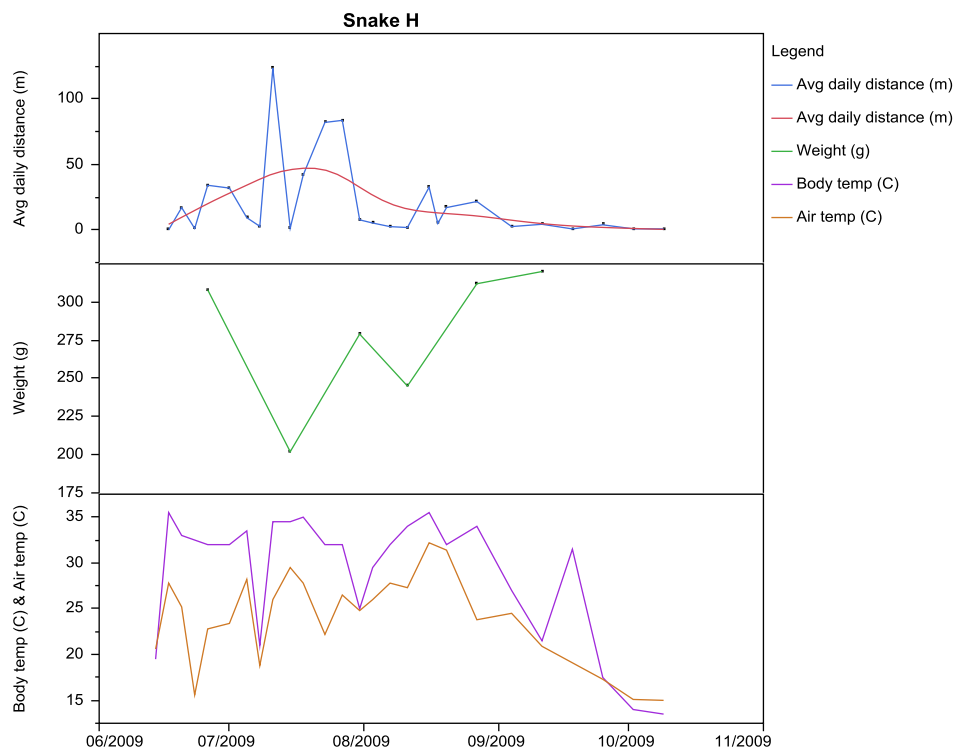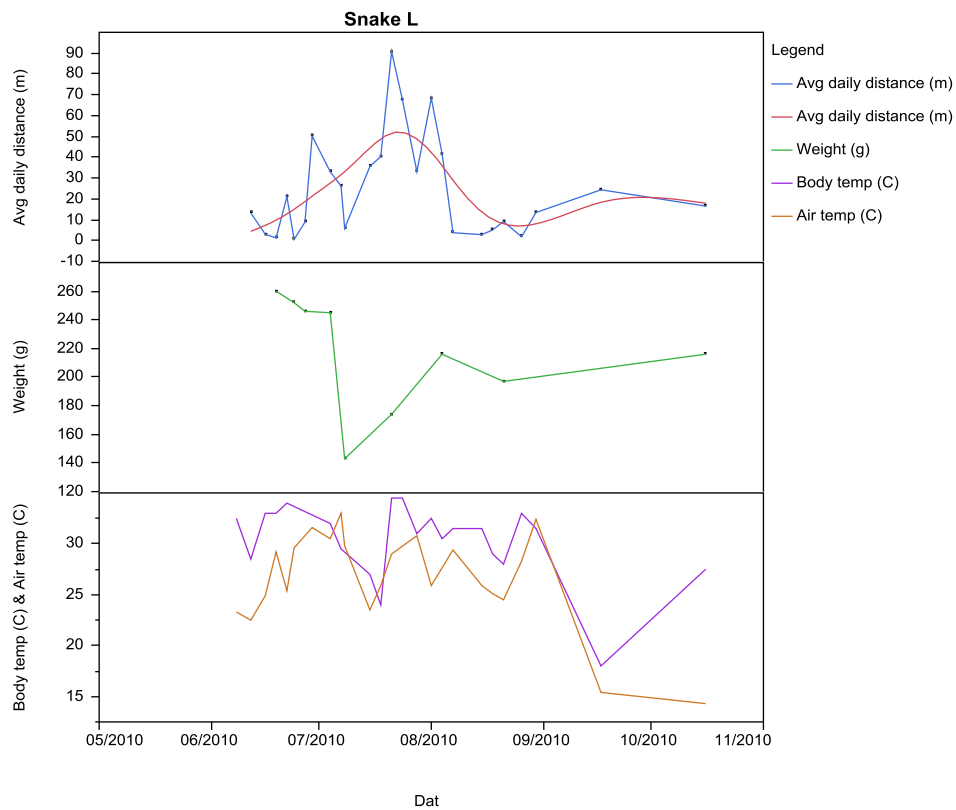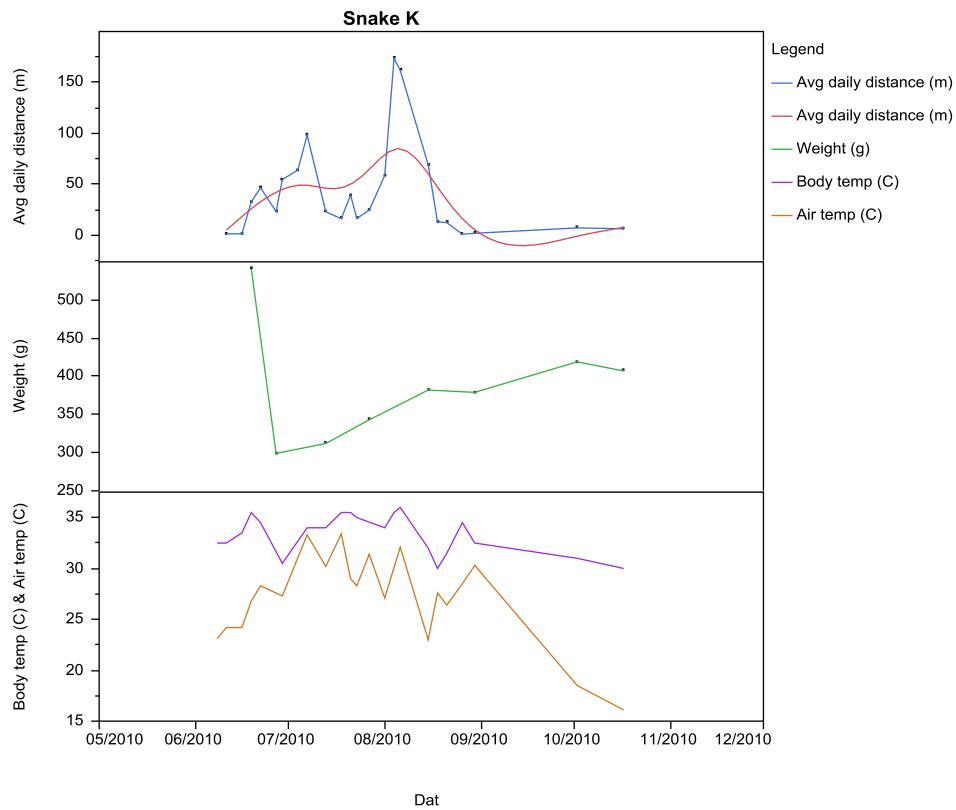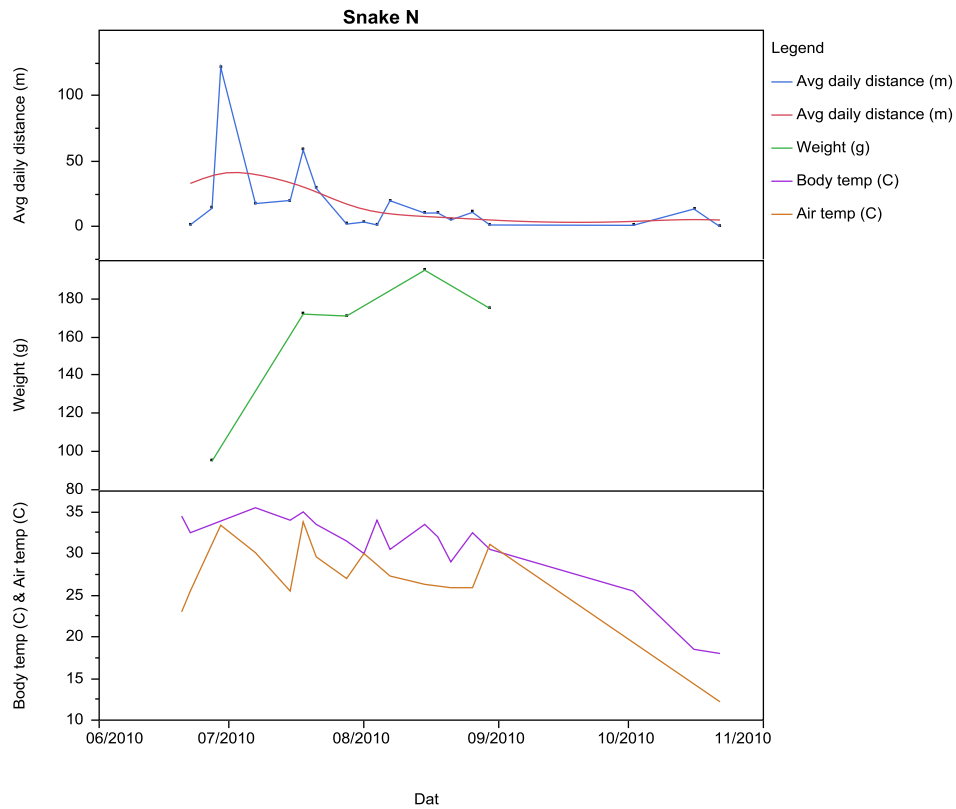
Figure 2.6b. Non-gravid females.
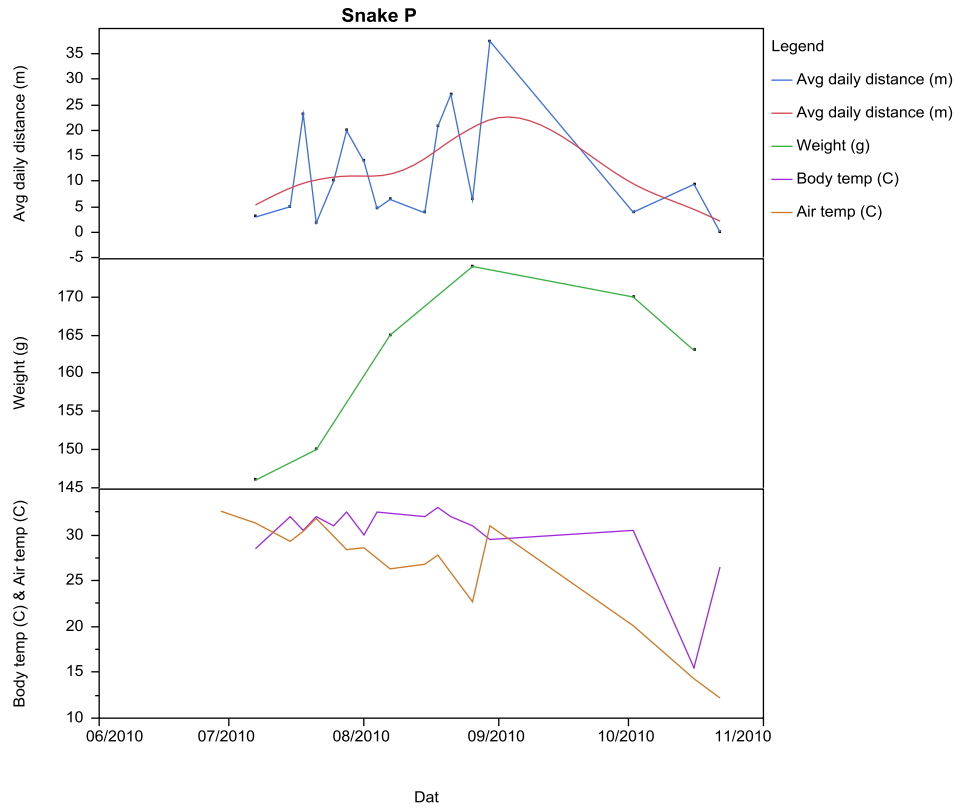
Figure 2.6c. Males

Snake I

Snake M

Snake O
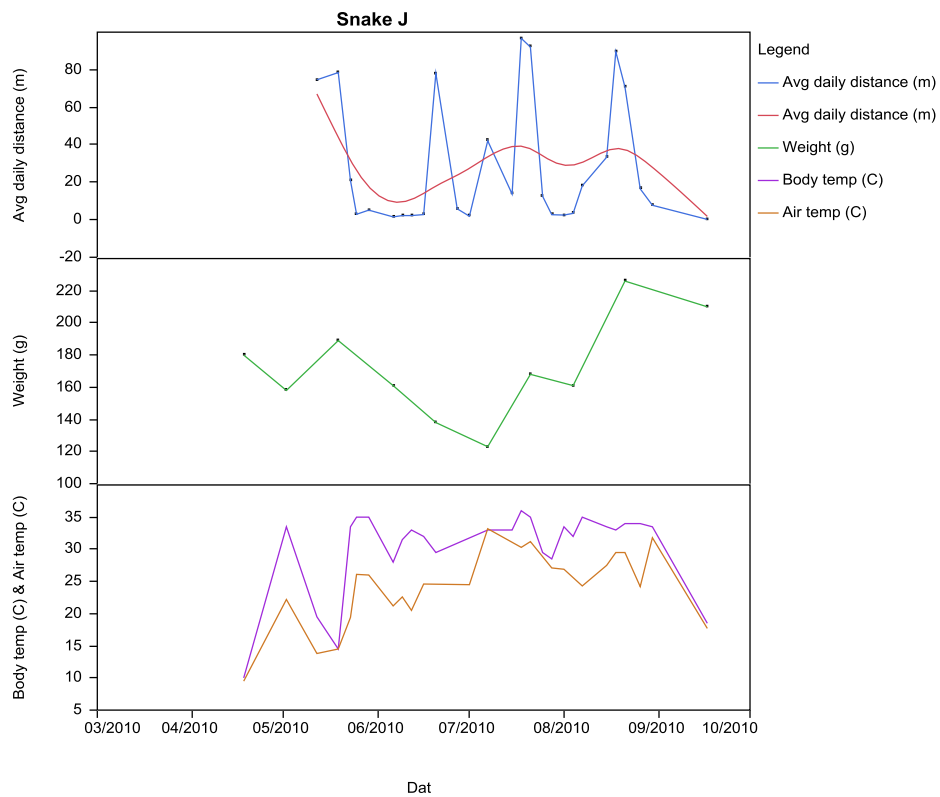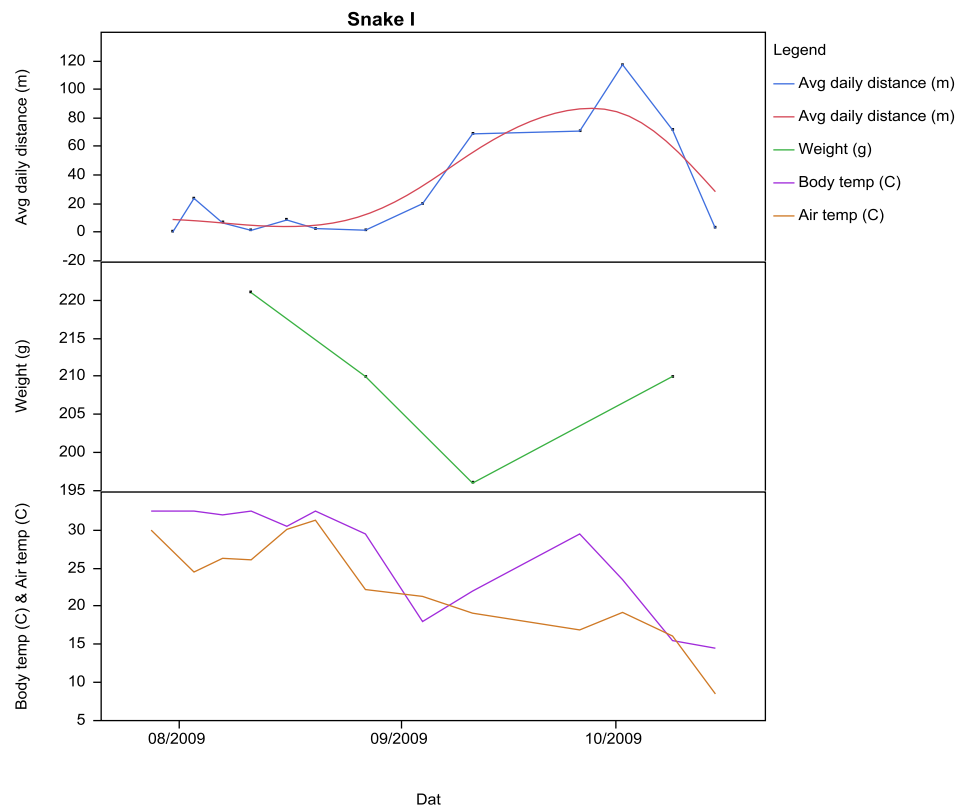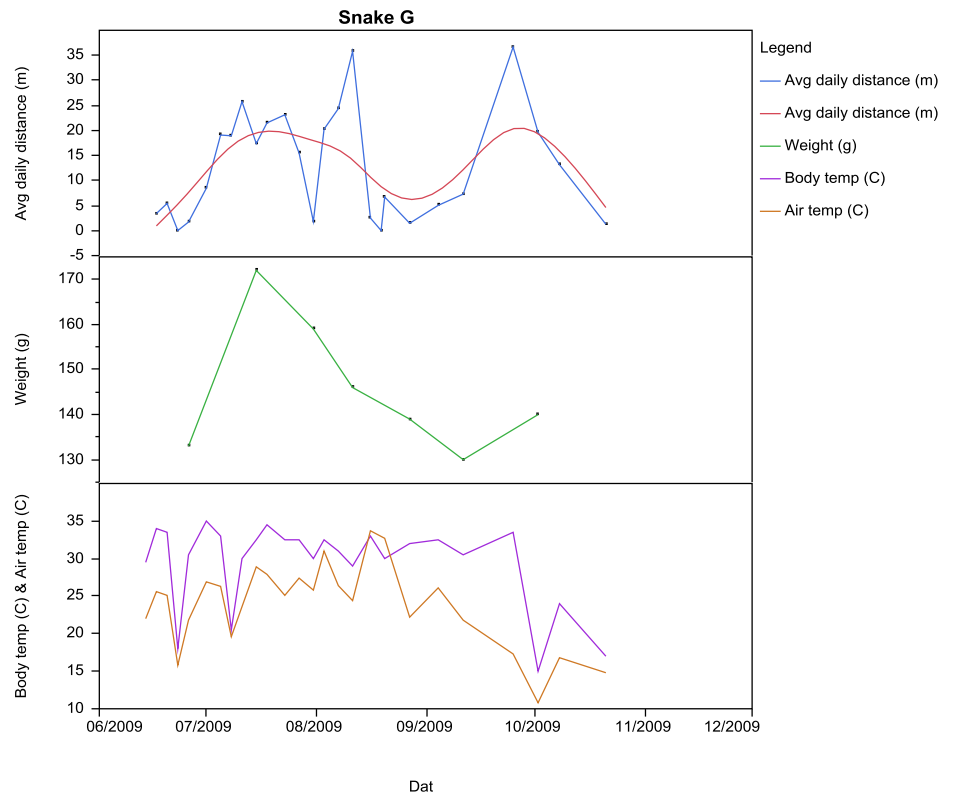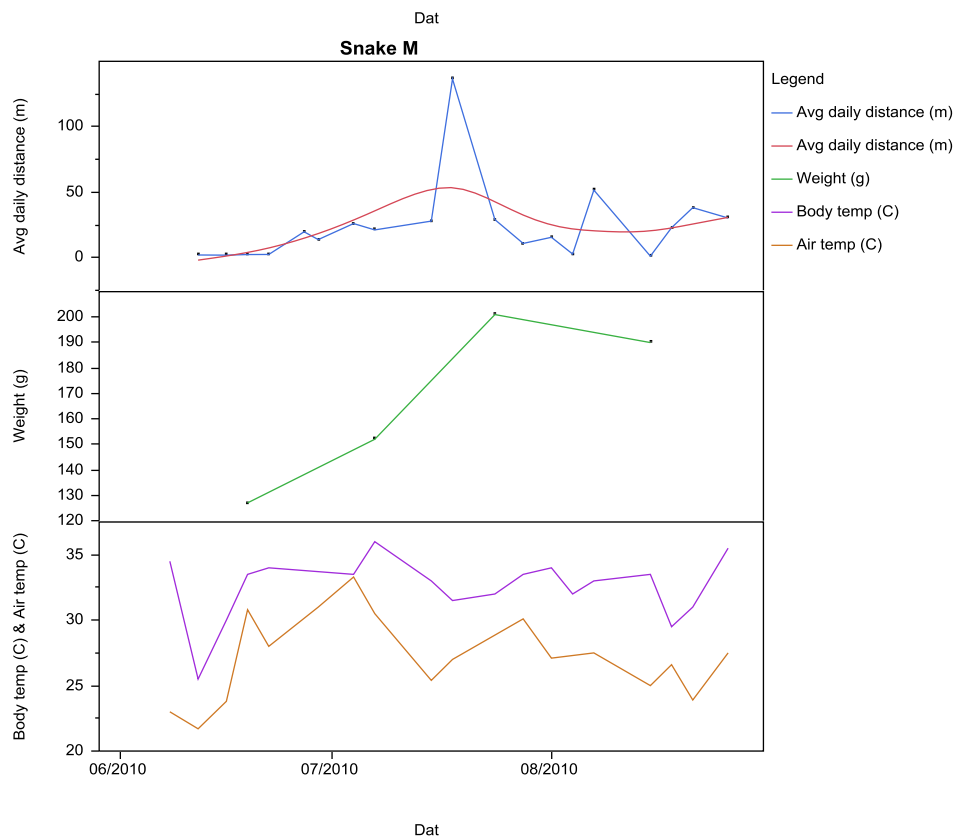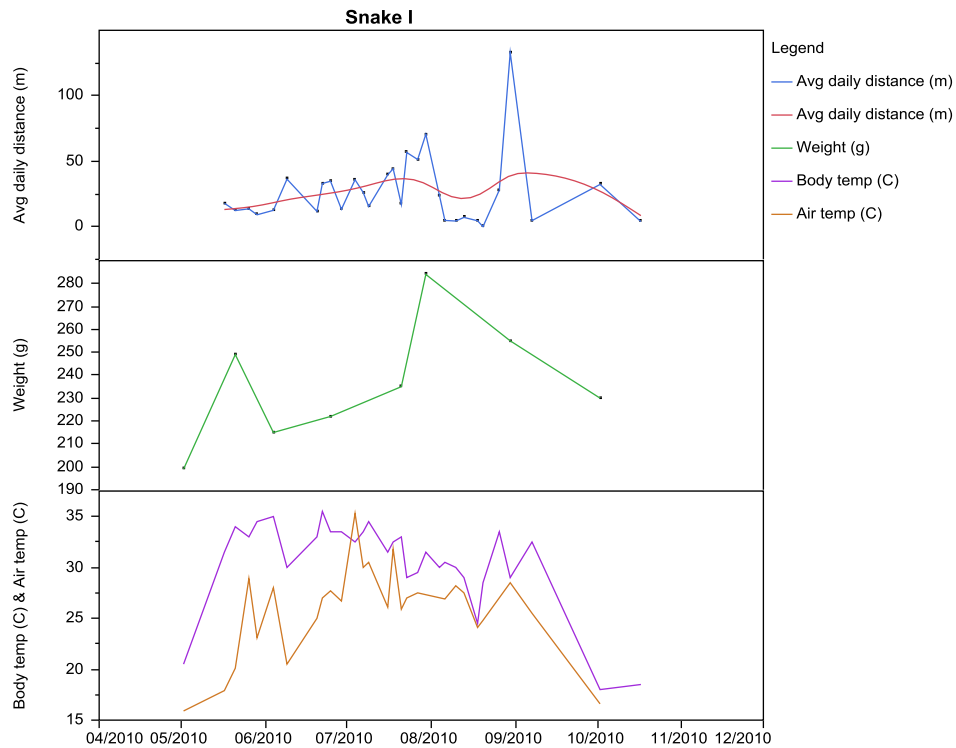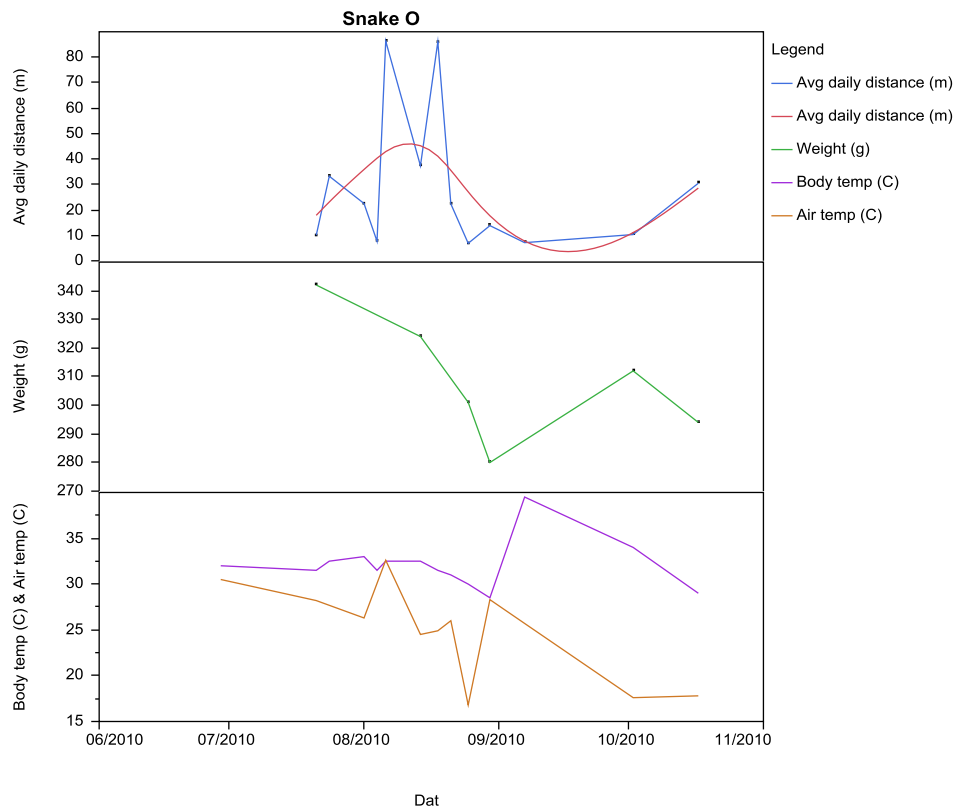
Figure 2.6. Average daily movement, body mass, body temperature, and ambient air temperature for *H. platirhinos* at Cape Cod National Seashore 2009-2010. The monthly tick-marks indicate the first of each month. a. Gravid females. The sharp drop-offs in mass represent the interval where snakes deposited eggs. This was usually followed by an immediate weight gain as a result of foraging. b. Non-gravid females. c. Males.
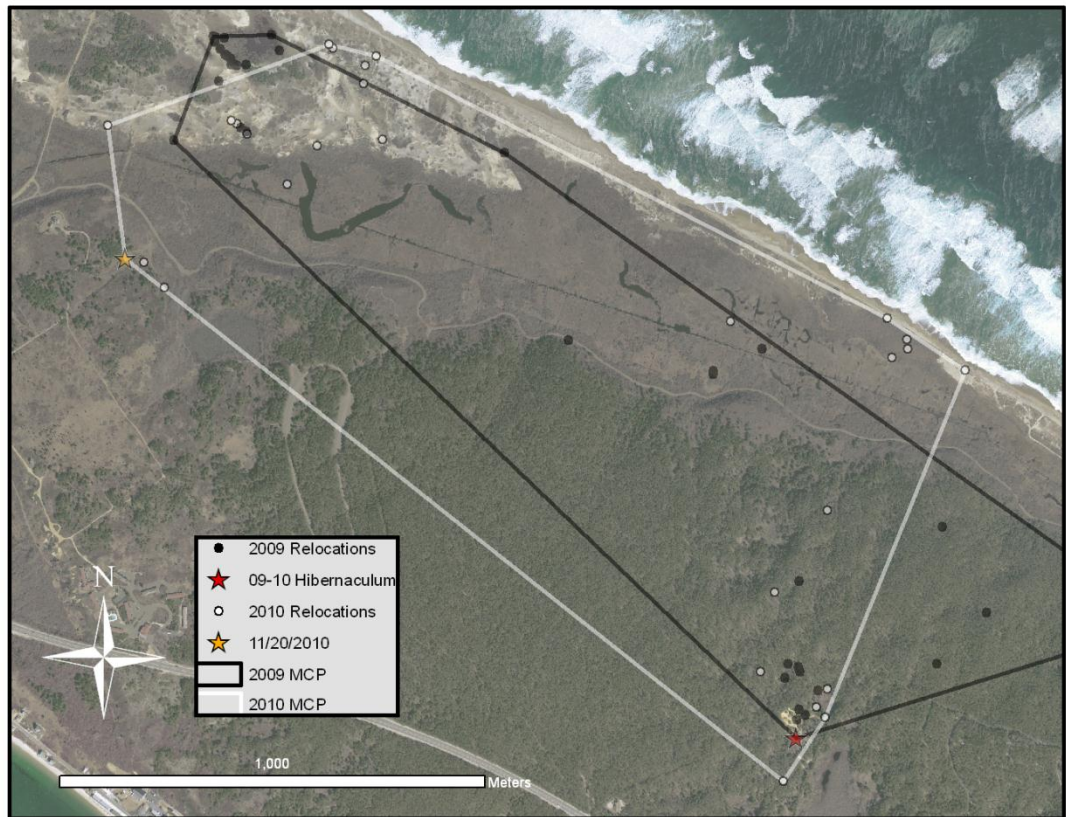
Figure 2.7a . Snake D.
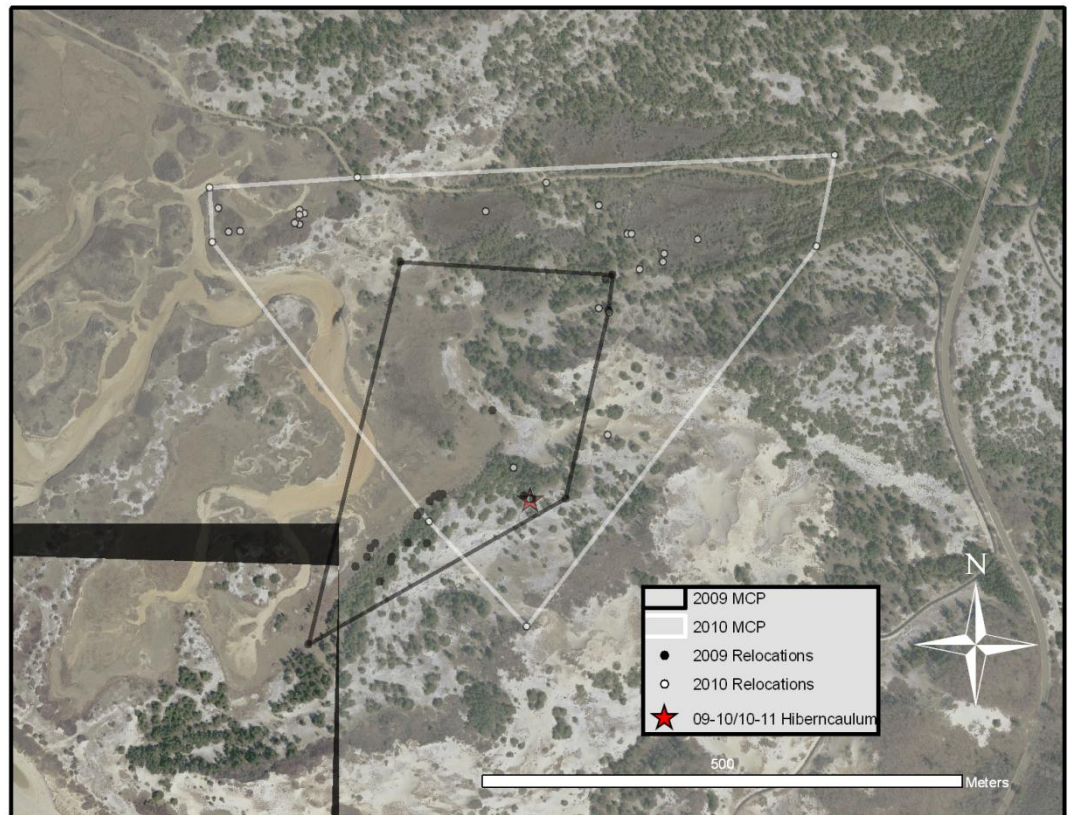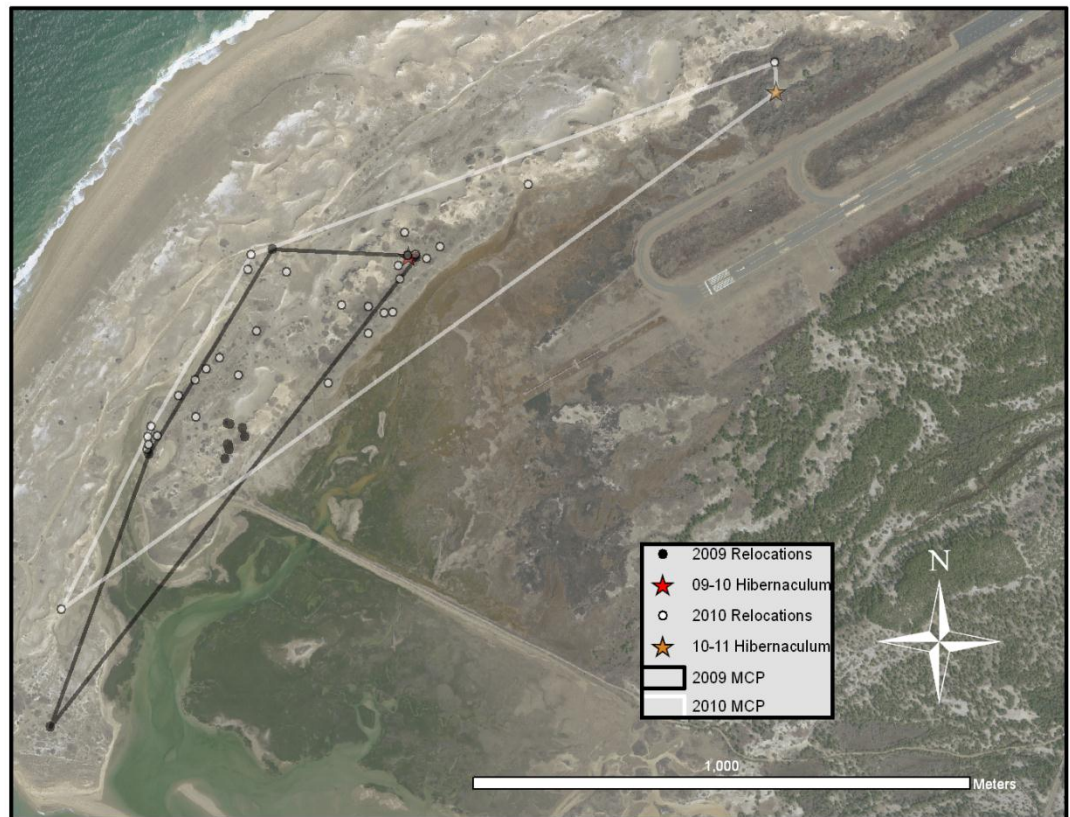
Figure 2.7b. Snake H.

Figure 2.7c. Snake I.

Figure 2.7. Annual minimum convex polygons (MCPs) for select *H. platirhinos* at Cape Cod National Seashore 2009-2010. Hibernacula are represented by stars. a. Snake D (female). b. Snake H (female). c. Snake I (male).